Purple Martin (*Progne subis*):
A Technical Conservation Assessment

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ACKNOWLEDGMENTS

AUTHOR'S BIOGRAPHY

David Wiggins developed an early interest in Ornithology. During his high school years, he worked as a museum assistant under George Sutton and Gary Schnell at the University of Oklahoma. He later earned degrees from the University of Oklahoma (B.Sc. in Zoology), Brock University (M.Sc.- Parental care in Common Terns, under the supervision of Ralph Morris), and Simon Fraser University (Ph.D. – Selection on life history traits in Tree Swallows, under the supervision of Nico Verbeek). This was followed by a National Science Foundation Post-doctoral fellowship at Uppsala University in Sweden, where he studied life history evolution in Collared Flycatchers, and later a Fulbright Fellowship working on the reproductive ecology of tits (Paridae) in Namibia and Zimbabwe. He currently splits time between ecological research programs in Sweden and North America.

COVER PHOTO CREDITS

Purple Martin (*Progne subis*) and breeding habitat in Region 2. Left photo: Breeding site in western Colorado. Photo courtesy of Scott Gillihan. Right photo: Male purple martin feeding nestling, Medicine Bow National Forest, Wyoming, July 2004. Photo courtesy of Frances and Janice Bergquist.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF PURPLE MARTIN

Purple martins (*Progne subis*) are classified as G5, or globally secure, by the Nature Conservancy, and aside from some areas where local populations have declined or are threatened (Pacific Northwest, Great Lakes), there does not appear to be any imminent threat to martin populations. The situation in the Rocky Mountains, however, is not easy to assess. Recent studies have confirmed widespread nesting in western Colorado, but with a total estimated population size of only 500 to 1000 individuals. Limited survey work in southern Wyoming in 2004 resulted in the discovery of at least one colony. This colony, located on the Medicine Bow National Forest, is the first known nesting in the state since the 1930s. Purple martins are relatively rare breeders in the Intermountain West, and local populations may thus be particularly susceptible to forest management practices that affect their primary breeding habitat, mature aspen (*Populus* spp.) stands. A lack of information on the ecology and life history of purple martins in mountainous areas hinders our ability to develop a regional conservation strategy.

The preferred habitat of purple martins in the Rocky Mountains is mature aspen forest with nearby meadows and open water. Martins nest in cavities in live aspen trees, which are currently not heavily harvested on National Forest System lands. However, there is some indication that aspen recruitment is low, primarily due to a lack of disturbance. The general rule of fire suppression on public lands has likely had a negative impact on purple martins by reducing the generation of new (post-disturbance) aspen stands, and by allowing encroachment of conifers into the open habitats preferred by foraging martins. Another key habitat component for purple martins is meadows, especially those with areas of open water. Such habitats may be degraded by forest management practices (e.g., road-building, timber harvesting) that alter the quality and distribution of water.

Formulating a coherent conservation plan, as well as providing management recommendations for purple martins, will require a considerable amount of further research into their biology in the Rocky Mountains. Although purple martins have been well-studied in eastern and central North America, the western subspecies has received little attention from researchers. Given the divergence in breeding ecology between eastern and western populations, this lack of study is an important issue. The habitat preferences of martins are still not fully understood, as many areas with apparently suitable habitat have not been colonized. In addition, there is virtually no information available on critical aspects of the life history of montane populations, including adult and juvenile survival, reproductive success, site fidelity, and dispersal. Thus, while improving habitat conditions will help, a full understanding of the conservation status of purple martins in mountainous areas of Region 2 will require further research on martin reproductive success, dispersal, and survival.

TABLE OF CONTENTS

EDITOR: Gary Patton, USDA Forest Service, Rocky Mountain Region

LIST OF TABLES AND FIGURES

Tables:

Figures:

INTRODUCTION

This conservation assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS) (**Figure 1**). The purple martin is the focus of an assessment because it is classified as a sensitive species in Region 2 and because it is a Management Indicator Species (MIS) on at least one forest unit in Region 2. In the National Forest System a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance and/or habitat capability that would reduce its distribution [FSM 2670.5 (19)]. A sensitive species requires special management, so knowledge of its biology and ecology is crucial. Within the National Forest System, MIS act as barometers for species viability at the forest level. They serve two functions: 1) to estimate the effects of planning alternatives on fish and wildlife populations [36 CFR 219.19 (a)(1)]; and 2) to monitor the effects of management activities on species via changes in population trends [36 CFR 219.19 (a)(6)].

This assessment addresses the biology, ecology, conservation, and management of the purple martin throughout its range, but with an emphasis on Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide land managers, biologists, and the public with a thorough discussion of the biology, ecology, conservation, and management of certain species based on current scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion
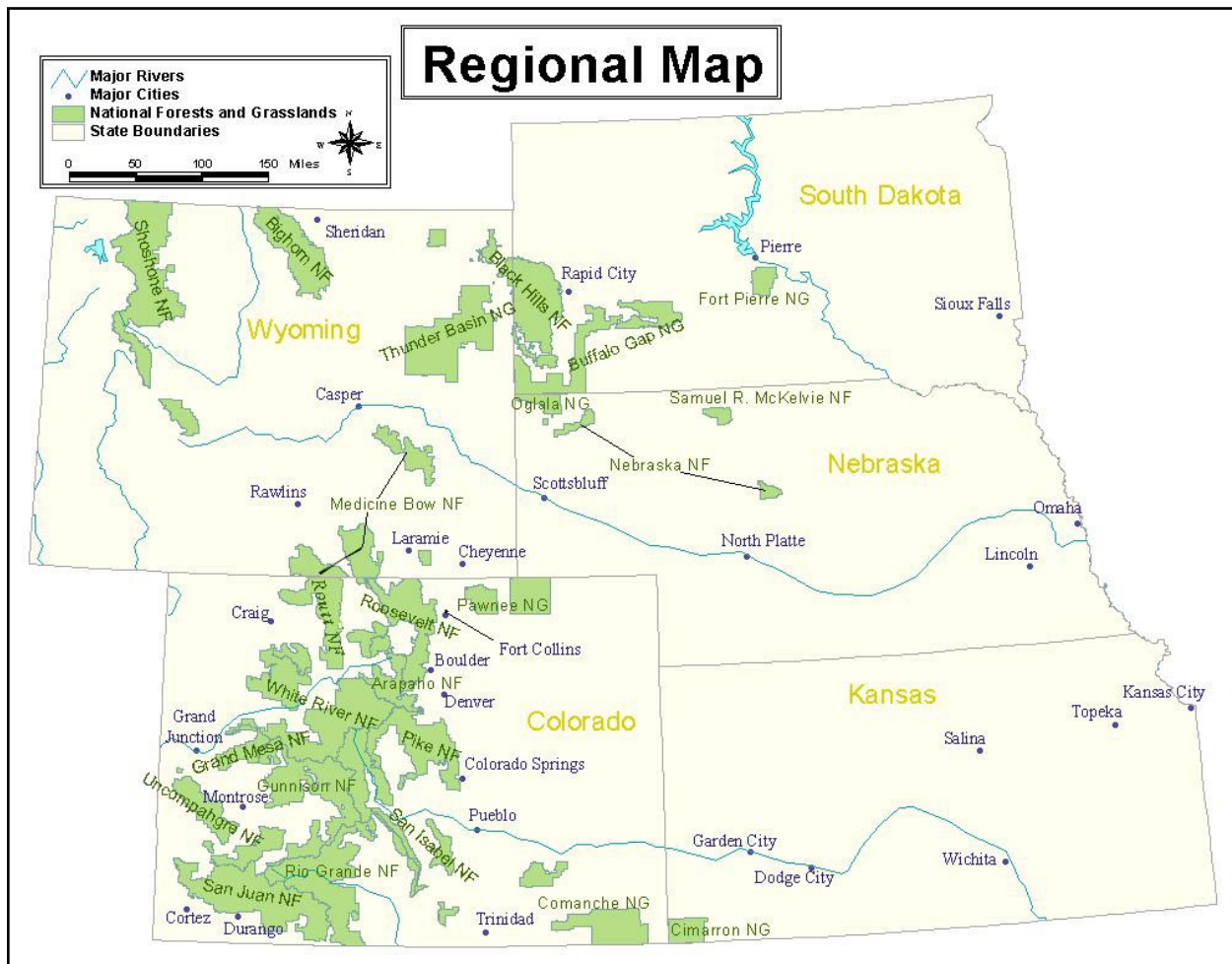

Figure 1. Map of National Forest System lands within USDA Forest Service Region 2.

of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop prescriptive management recommendations. Rather, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, it cites management recommendations proposed elsewhere and examines the success of those that have been implemented.

Scope and Limitations of Assessment

The purple martin conservation assessment examines the biology, ecology, conservation, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. The majority of the literature on the species originates from studies in central and eastern North America. Martin populations in the Rocky Mountains, the desert southwest, and particularly the Pacific Northwest have been poorly studied. Consequently, much of the information in this assessment pertains to eastern populations. This document places that literature in the ecological and social context of the Rocky Mountain Region, and I have attempted to highlight those sections where clear differences exist between eastern and western populations, as well as among the three subspecies. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of purple martins in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting the synthesis, but placed in current context.

In producing the assessment, I reviewed refereed literature, non-refereed publications, research reports and data accumulated by resource management agencies. Not all publications on purple martins are referenced in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were used when refereed information was otherwise unavailable, but they were regarded with greater skepticism.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct experiments that produce clean results in the ecological sciences. Often, observations, inference, good thinking, and models must be relied on to guide our understanding of ecological relations. Confronting uncertainty then is not prescriptive. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate.

Publication of Assessment on the World Wide Web

To facilitate use of species conservation assessments, they are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, Web publication will facilitate revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Conservation assessments developed for the Species Conservation Project have been peer reviewed prior to their release on the Web. This report was reviewed through a process administered by the Society for Conservation Biology, employing two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Purple martins are not considered threatened at the global scale, having received a conservation ranking of G5 (globally secure) from the Nature Conservancy (www.natureserve.org/explorer). In Canada, they are not considered threatened at the federal level (Committee on the Status of Endangered Wildlife in Canada 2004), but the species is red-listed (denoting threatened or endangered status) by the provincial government in British Columbia (Fraser et al. 1997). Purple martins were not included in the recently published "Bird of Conservation Concern" by the U.S. Fish and Wildlife

Service (2002). Still, state Natural Heritage Programs have designated purple martins as critically imperiled (S1) in Idaho, imperiled (S2) in Utah, and vulnerable (S3) throughout much of the rest of the western United States, including Colorado (**Figure 2**). Within Region 2, purple martins are listed by USFS Region 2 as a sensitive species and as a MIS on the White River National Forest.

A summary of the management status of purple martins within state and regional Partners In Flight (PIF) bird conservation plans is presented in **Table 1**. Martins are listed as a Priority Species in the Colorado PIF plan (Beidleman 2000), but they are not a Priority Species in the Wyoming PIF plan (Cervoski et al. 2001). PIF plans for other states within Region 2 have not been published. The Arizona PIF plan (Latta et al. 1999) lists both subspecies, *Progne subis hesperia* and *P. s. arboricola*, Priority Species

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Currently, there are no published management plans or conservation strategies for purple martins. However, there is a network of concerned volunteers, coordinated by the Purple Martin Conservation Association (PMCA; www.purplemartin.org), that promotes continent-wide interest in improving conditions for purple martins, primarily nesting conditions. The PMCA web site provides a wealth of information on all aspects of martin biology.

Although not designed as a range-wide or even a regional management plan, state-based PIF management recommendations for purple martins are currently the only published frameworks from which regional plans could be constructed. These PIF recommendations and
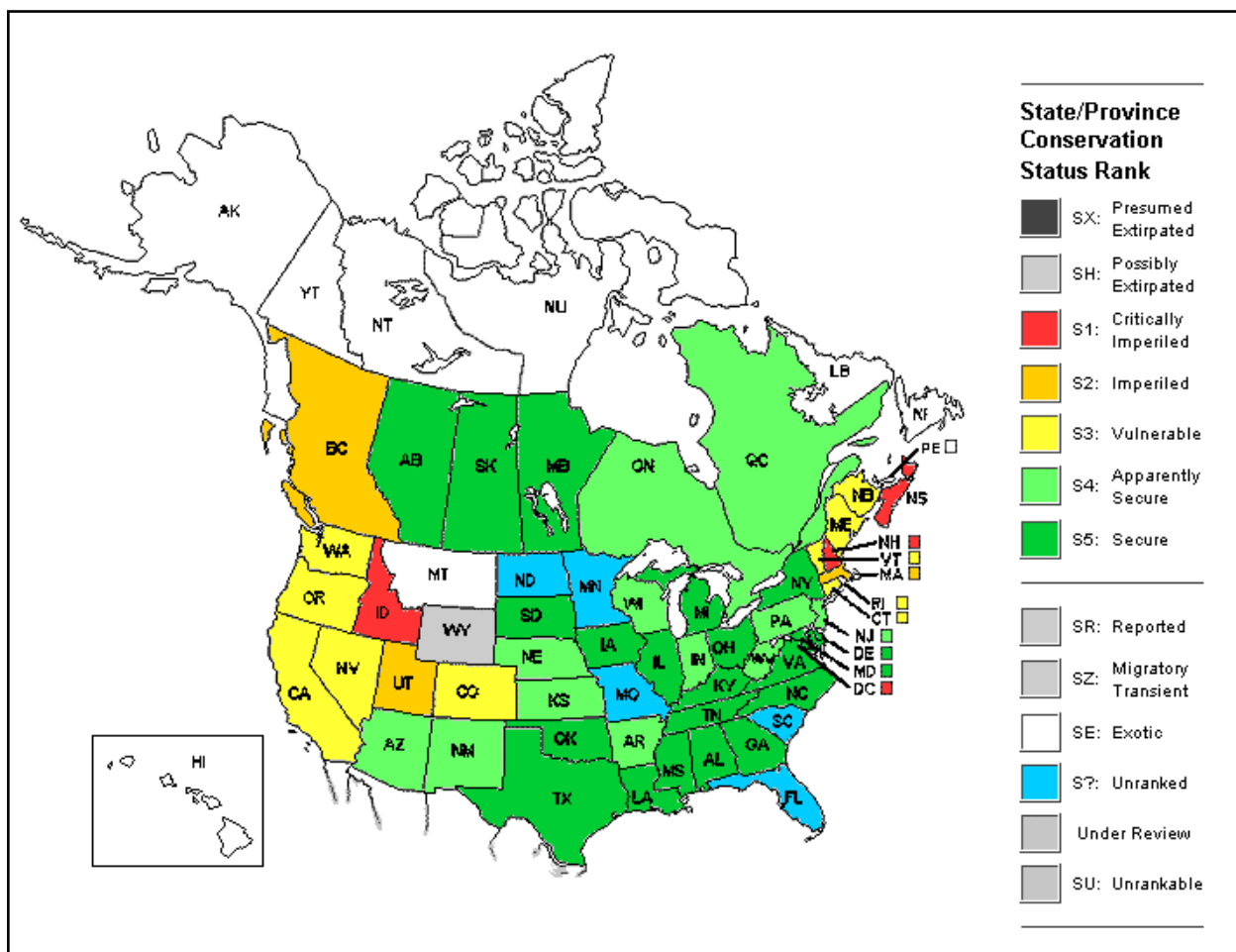
Figure 2. Status of purple martins in North America based on the Natural Heritage Program (NatureServe Explorer 2003).

Table 1. Management status of purple martins according to Partners in Flight (PIF) bird conservation plans of states within and surrounding USDA Forest Service Region 2.

State	Status	Citation
Colorado*	Priority Species (Aspen woodlands)	Beidleman 2000
Kansas*	State PIF plan not published	
Wyoming*	Not a Priority Species	Cervoski et al. 2001
Nebraska*	State PIF plan not published	
South Dakota*	State PIF plan not published	
Montana	Not a Priority Species	Casey 2000
New Mexico	Not a Priority Species	Rustay 2001
Utah	Not a Priority Species	Parrish et al. 2002
Idaho	Not a Priority Species	Ritter 2000
Arizona	Priority Species (Pine woodlands, Sonoran desert scrub)	Latta et al. 1999

*Region 2 states

the management suggestions provided by Gillihan and Levad (2002) are listed in **Table 2**.

Biology and Ecology

Systematics

Two subspecies of purple martin were recognized by the American Ornithologists' Union (1957); most of the North American populations were assigned to *Progne subis subis*, and populations found in southern Baja California, south-central Arizona, and southward into Sonora, Mexico were assigned to *P. s. hesperia*. *Progne subis arboricola* was later recognized as the breeding martin in all of montane, western North America (Behle 1968). There is little clear morphological variation among the three subspecies; *P. s. hesperia* tends to be smaller, and *P. s. arboricola* females tend to have whiter foreheads. The three subspecies are more easily separated on ecological grounds, with *P. s. subis* being a lowland, highly colonial nester, *P. s. hesperia* nesting solitarily in large desert cacti, and *P. s. arboricola* being primarily solitary (occasionally loosely colonial) nesters in montane aspen forests as well as coastal situations in the Pacific Northwest. There remains considerable uncertainty regarding the relationship of the Pacific Northwest, Rocky Mountain, and southwestern desert forms (Brown 1997).

Nominate race: *Progne subis subis* Linnaeus.

Distribution and abundance

Global perspective

Purple martins breed throughout most of eastern North America, along the coast of the Pacific Northwest, patchily in the southern Rocky Mountains and Sierra Madre Occidental, and into low elevation desert areas of Arizona, Baja California, and southwestern Mexico (**Figure 3**). There has been no apparent distributional change in central and eastern North America, but some historical records indicate that purple martins were formerly common in areas where they are now largely absent (e.g., Nebraska panhandle). Such localized changes in distribution may stem from the shift from nesting in tree cavities to nesting in man-made structures. Data from Breeding Bird Surveys (BBS) suggest that purple martin populations are relatively stable (**Table 3**), with threatened populations only on the Pacific Coast, in New England, and in Maritime Canada (**Figure 4**; see the Population trend section below). Their status in the Rocky Mountains and along the Pacific Coast is much more difficult to measure, as martins occur at relatively low densities in these areas.

Purple martins winter in central South American lowlands from eastern Bolivia to southern Brazil and (rarely) northern Argentina. Their winter distribution is somewhat problematical due to identification problems with the South American *Progne* species complex (see discussion in Brown 1997). The Amazon River basin appears to be a major staging area both in spring and fall migration periods (Ridgely and Tudor 1989).

Most historical works suggest that purple martins were relatively common breeding birds within and near Region 2. For example, Ducey (2000) summarized a number of breeding records from expeditions in the 1800s in Nebraska. One expedition noted purple martins as "abundant" in the Black Hills of South Dakota in August 1873 (Grinnell 1875). Purple martins apparently increased in abundance in southern Manitoba in the late 1800s, when they were still nesting

Table 2. Summary of published management recommendations for purple martins within state Partners in Flight bird conservation plans and from Gillihan and Levad (2002).

State	Recommendations	Presumed benefits	Citation
Colorado	Retain 8 to 12 live, cavity-bearing trees or large diameter snags per 4 ha (10 ac) of aspen woodland.	Provide suitable nest sites.	Beidleman 2000
	Maintain natural disturbance regimes in aspen communities.	Ensure future supply of potentially suitable nest sites.	
Colorado	Post nest trees with wildlife tree signs; protect nest area by limiting harvest of large diameter aspens.	Prevents harvesting of trees in immediate nest area.	Gillihan and Levad 2002
	Incorporate the retention of large, live aspen trees (with cavities) into forest management plans.	Current management plans typically only recognize snags - live trees are a critical resource for martins.	
	Protect unoccupied sites with suitable habitat characteristics.	Provide potential new breeding sites.	
Arizona	1) Pine populations (*arboricola* subspecies):		Latta et al. 1999
	Maintain and create tall (150-200 ft) snags in forest openings and near water.	Increase nest site availability.	
	Use prescribed fire and mechanical thinning to reduce tree density, being careful to protect snags from burning/cutting.	Improve habitat quality.	
	2) Sonoran desert populations (*hesperia* subspecies):		
	Encourage landowners/managers to maintain large saguaros and to increase saguaro recruitment success.	Increase and ensure long-term availability of nest sites.	

in tree cavities (Thompson 1891). More recent records within Region 2 suggest little change, with the possible exception of Nebraska (BBS data; **Table 3**). However, population status is difficult to track given the relatively low numbers of birds in most Region 2 states, as well as the BBS methodology (where surveys are typically undertaken on rural routes – areas where martins are now scarce).

Regional distribution and abundance

In Colorado, purple martins are largely restricted to western slope aspen forests, and as far as is currently known, they are patchily distributed (see GAP maps for Utah and Colorado projected distributions in **Figure 5** and **Figure 6**). Recent surveys in southern Wyoming have established at least one breeding colony in the south-central portion of the state (Faulkner and Levad 2004; see below). Purple martins are common breeders throughout low elevation areas in central and eastern Kansas, Nebraska, and South Dakota (**Figure 7**; Sauer et al. 2003). As mentioned previously, populations breeding on the Great Plains represent a subspecies different from those breeding west of the continental

divide, with distinct differences in ecology. The historical and current distributions and abundance in Region 2 are as follows:

South Dakota: Recent treatments suggest that purple martins are relatively common breeders in eastern South Dakota, but uncommon in central parts of the state and accidental in the west (Peterson 1995, Tallman et al. 2002). Although there is no good historical reference regarding the status of breeding purple martins in South Dakota, two authors reported that the species was formerly "abundant" (Grinnell 1875) or "common" (Visher 1909) in the Black Hills. Although the former report was based on sightings in August, it appears likely that martins nested in suitable areas of the Black Hills. However, there are no records of the species breeding in the Black Hills since Visher's report in 1909 (Pettingill and Whitney 1965, A. Panjabi personal communication 2004).

Wyoming: Purple martins have always had an uncertain breeding status in the state. Although Knight (1902) suggested that they were "probably a summer resident", he gave no definitive nesting records, but
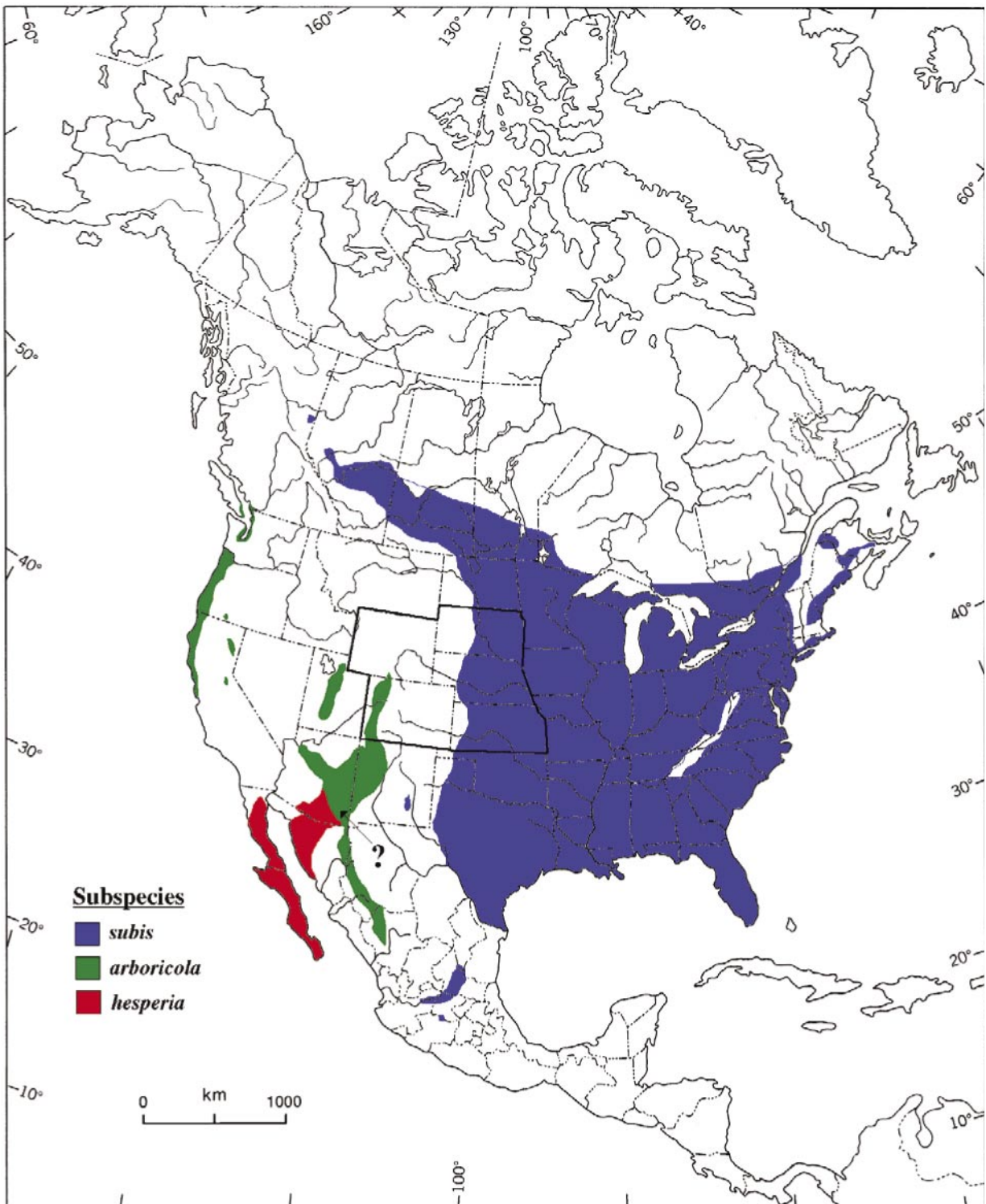
Figure 3. Range of purple martins in North America, modified from Brown (1997). The area bounded in black represents the approximate boundaries of Region 2. Note that the exact distribution of subspecies is problematical in several areas (see text and Brown 1997).

Table 3. Purple martin trend results from North American Breeding Bird Surveys. Data were taken from Sauer et al. (2003) and focus on USDA Forest Service Region 2 and surrounding areas. Trend indicates the percentage change per year.

Region	1966-1979			1980-2002			1966-2002		
	N	Trend	*P*	*N*	Trend	*P*	*N*	Trend	*P*
South Dakota*	5	6.8	0.65	4	- 6.7	0.42	6	- 6.8	0.06
Nebraska*	6	33.8	**0.05**	7	- 5.7	0.32	10	- 3.4	0.19
Wyoming*	—	—	—	—	—	—	—	—	—
Colorado*	—	—	—	8	7.7	0.32	8	9.0	0.27
Kansas*	15	- 0.2	0.97	20	2.5	0.18	26	1.1	0.57
Oklahoma	23	9.7	**0.02**	33	3.2	**0.00**	40	3.8	**0.00**
New Mexico	—	—	—	6	10.0	**0.01**	7	1.0	0.82
Arizona	4	- 9.1	0.16	12	- 1.7	0.45	13	0.9	0.86
Utah	—	—	—	3	14.1	0.37	3	10.2	0.47
Iowa	27	1.8	0.64	24	- 7.3	0.12	32	- 6.3	**0.01**
Missouri	32	11.3	**0.03**	54	- 0.1	0.97	56	1.3	0.28
Arkansas	28	4.0	0.07	32	- 0.9	0.53	33	0.6	0.50
U.S. Fish and Wildlife Service Region 6	33	4.9	0.14	51	0.3	0.81	65	- 0.6	0.63
United States	952	3.3	**0.00**	1365	- 0.5	0.16	1549	- 0.1	0.78
Canada	48	2.2	0.29	100	**0.00**	0.97	117	0.4	0.67
Survey-wide	1000	3.3	**0.00**	1465	- 0.5	0.18	1666	- 0.1	0.85

*Region 2 state.

rather scattered historical records for spring and summer, largely in eastern Wyoming. Several studies in the 1990s concluded that the species did not breed in Wyoming (Scott 1993, Dorn and Dorn 1999, Cervoski et al. 2001). However, Scott (1993) suggested that martins may nest in mountainous areas of southwestern Wyoming, and recent surveying work has established at least one breeding site on the Medicine Bow National Forest in south-central Wyoming (Faulkner and Levad 2004). This raises the possibility that scattered colonies may exist in mountainous areas of Wyoming. There is little evidence of any historical change in the breeding status in the state, as there is only a single earlier reported case of nesting, that of a pair along the Laramie River (McCreary 1939).

Nebraska: There are recent breeding records of purple martins throughout the eastern two-thirds of the state, but the species is apparently absent in the panhandle region and generally rare in the western half of the state (Molhoff 2001, Sharpe et al. 2001). Although Molhoff (2001) suggested that there has been no apparent historical change in distribution, there are indications that martins were formerly much more common in western Nebraska (or, alternatively, that they were much less common in eastern Nebraska). Ducey (2000, p.89) notes a record of purple martins

breeding in the southwestern corner of the panhandle in 1845 (Carelton 1983) and also the possibility that they nested in the Pine Ridge country (Ducey 2000, p. 150). Hayden (1863) stated that they were most common in riparian areas in the northwestern part of the state, indicating that purple martins once bred along the river valleys and forested areas of the Nebraska panhandle, an area where they are now absent as breeders.

Colorado: In Colorado, purple martins were historically noted as rare and local, occurring primarily on the western slope of the mountains (Sclater 1912). Bailey and Niedrach (1965) noted it as a "rare summer resident and local breeder in western counties". Although the first record of breeding came from the mesa country in the southeast part of the state, (Las Animas County, Aiken, cited in Sclater 1912) recent breeding records are all from the western slope, west of approximately 107° longitude (Andrews and Righter 1992, Levad 1998). Annual nest searches by the Rocky Mountain Bird Observatory continue to expand the known breeding range in western Colorado, which now extends from Routt County in the northwest, southward through the Flat Top range, the Uncompahgre Plateau, and into the San Juan Mountains of southwestern Colorado (Gillihan and Levad 2002).
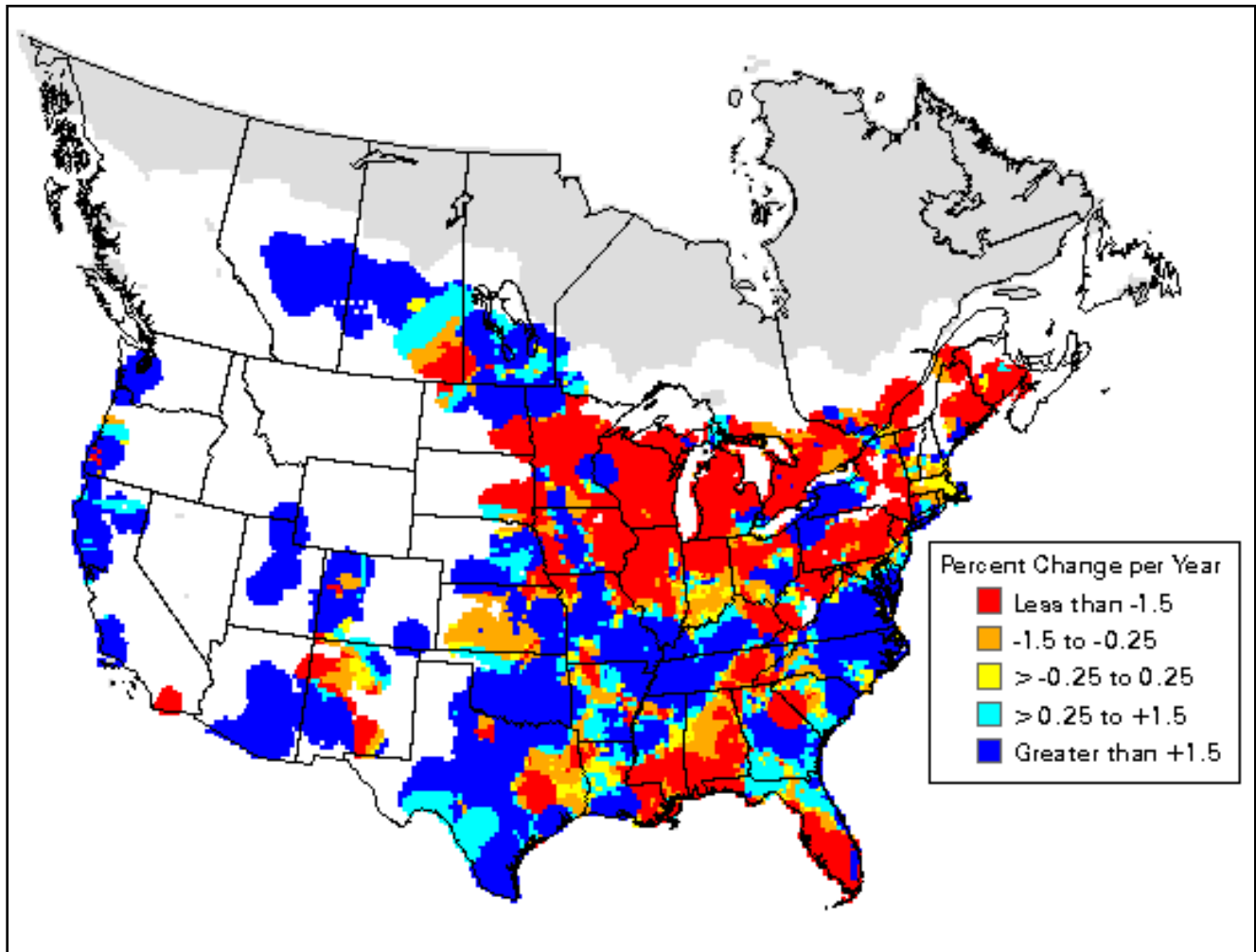
Figure 4. Mean annual trends in the number of purple martins observed on Breeding Bird Surveys from 1980 to 2003. Data are from Sauer et al. (2003).

Kansas: Thompson and Ely (1992) report that purple martins are common summer residents in eastern Kansas, but uncommon and local summer residents in the west. Purple martins were largely absent from the western third of Kansas during recent breeding bird atlas work there (Busby and Zimmerman 2001). However, the authors suggested that martin colonies (in towns) in western counties may have been overlooked.

Within Region 2, the distribution of purple martins does not appear to have changed drastically since the mid-1800s, when the earliest records were kept). However, the possibility remains that the species was once a breeder in western South Dakota (Black Hills area) and western Nebraska (Pine Ridge and southern panhandle), areas where the species no longer breeds. Surprisingly, Morton (1988) suggests that the available evidence points to a lower current abundance of purple martins in North America relative to the situation in the

1800s. In the Great Plains and in most of eastern North America, the species is now restricted to breeding in man-made nesting compartments, and competition for nesting sites with introduced house sparrows (*Passer domesticus*) and European starlings (*Sturnus vulgaris*) has been cited as a potential contributor to declines in martin abundance (Brown 1997). The historical abundance in the West is much more difficult to assess, as there are few historical records of martins nesting in the Rocky Mountains.

Regional discontinuities in distribution and abundance

Purple martins breed relatively contiguously over most of the central and eastern portions of South Dakota, Nebraska, and Kansas. In these states, they are generally common in the east, and become uncommon (central) to rare further west. Similarly, martin

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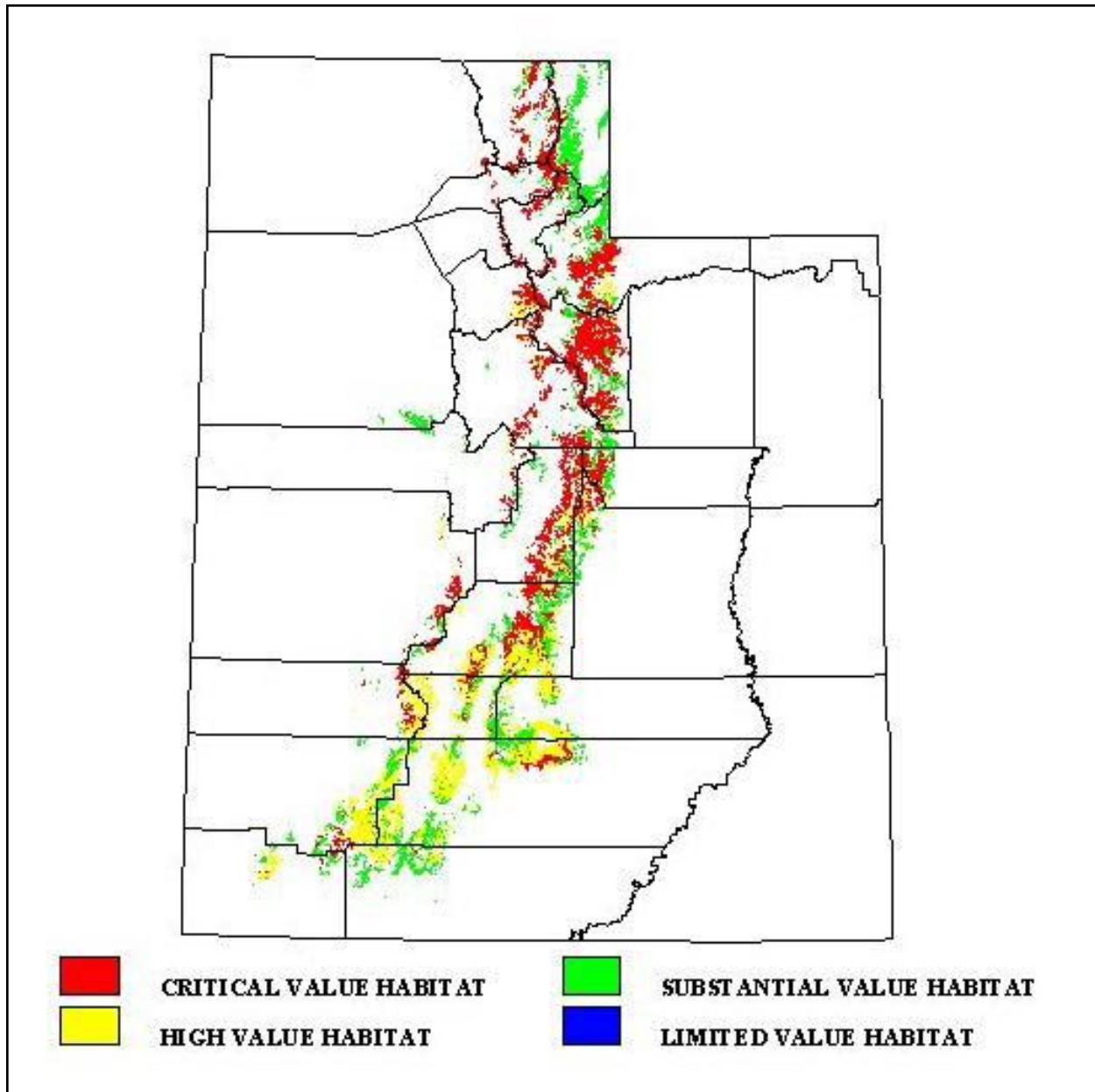
Figure 5. Modeled potential suitable habitat for purple martins in Utah, based upon GAP analysis.

abundance shows a weak decline from south to north, with the species more common in eastern Kansas than in areas to the north (**Figure 7**). There is then a large gap in the distribution until the species (*Progne subis arboricola*) occurs again in south-central Wyoming and northwestern Colorado. From there southward, martins are distributed patchily in open, mountainous areas from about 7900 to 9900 ft. in elevation (Gillihan and Levad 2002). In western Colorado, martins occur at much lower densities than they do on the central and eastern Great Plains. Gillihan and Levad (2002) suggested that the total Colorado population likely numbered between 500 and 1000 birds.

Population trend

Data from the BBS (Sauer et al. 2003) are summarized in **Table 3**. Within Region 2, martins appear to be declining (since 1980) in South Dakota and Nebraska, but relatively small samples sizes weaken the statistical power of such analyses. BBS trend analyses suggest that from 1980 to 1996, there were areas of both population declines and increases in South Dakota, Nebraska, and Kansas (**Figure 4**). During the same period, similar analyses in Colorado suggested increases in the northwest, but decreases in the southwest. However, the extremely small sample
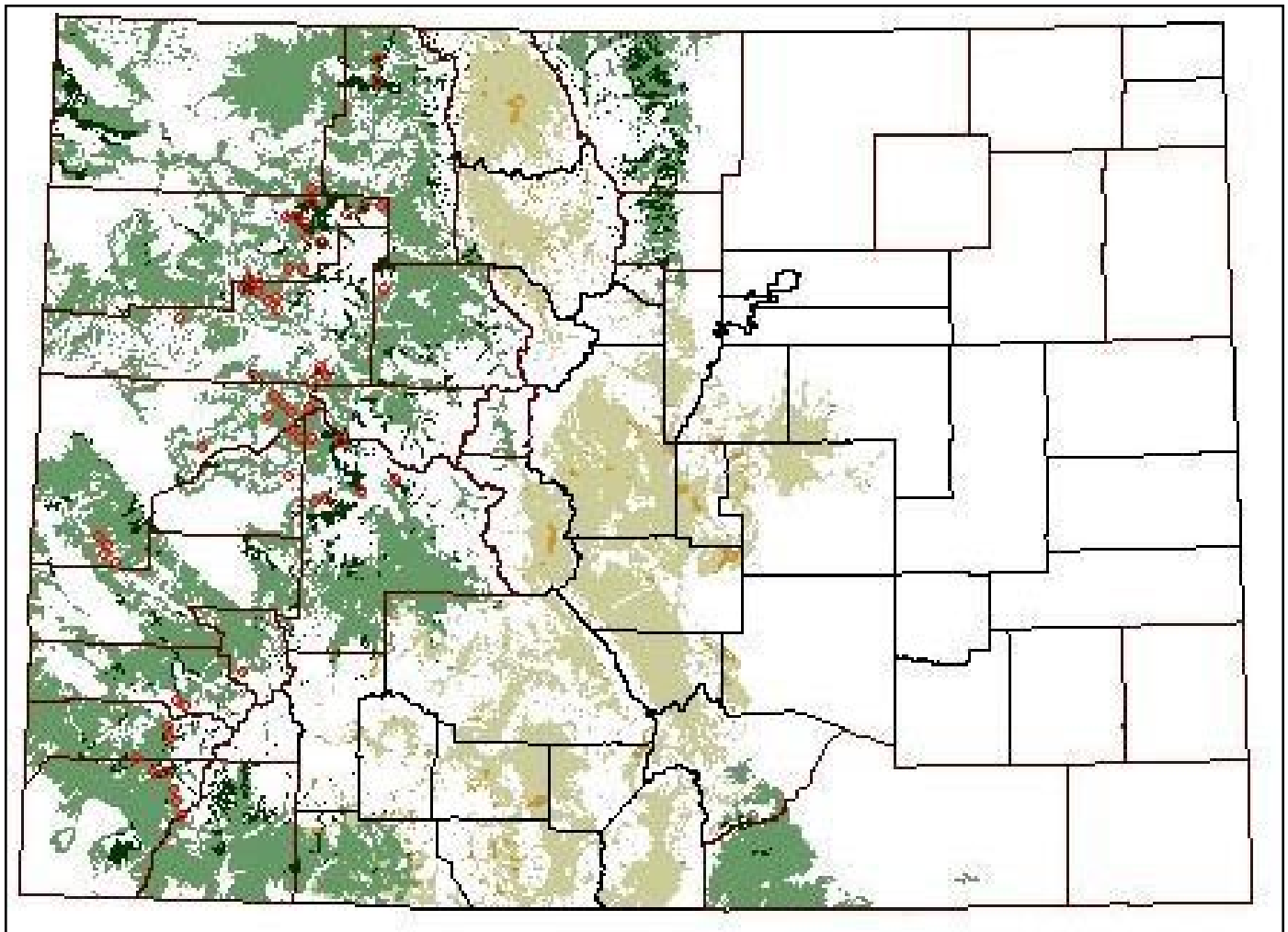
Figure 6. Modeled potential suitable habitat for purple martins in Colorado, based upon GAP analysis. Light green areas represent predicted suitable habitat (with aspen forest in dark green), while beige areas represent possibly suitable habitat. The red circles represent known breeding localities as of 2002 (taken from Levad 2003).

sizes in Colorado make such analyses statistically unsound. In fact, purple martins were not even considered a breeding species in Colorado as recently as 1978 (Kingery and Graul 1978).

As mentioned above, problems associated with BBS methodology and with small sample sizes (in the case of purple martins) suggest that the BBS trend results be viewed with some degree of uncertainty. Range-wide, the only areas showing statistically significant declines in martin abundance are the Great Lakes and St. Lawrence River plain areas. The recent negative trends in South Dakota and Nebraska suggest the need for continued close monitoring of those populations. The situation in Colorado is very different; the known martin population continues to increase as dedicated survey efforts find new breeding sites each

year (Levad 2003). Assessing population trends in Colorado will not be possible until repeated sampling of the known breeding sites has been carried out for several years.

There are no data available to assess changes in population densities on purple martin wintering grounds in South America.

Activity pattern and movements

Purple martin migratory behavior is relatively well known. In spring, adult (>1 year old) males are the first to arrive at breeding sites, followed by adult females, and subsequently (up to two months later) by first year birds of both sexes (Morton 2003). On the Great Plains in Region 2, males arrive in March, and the peak of
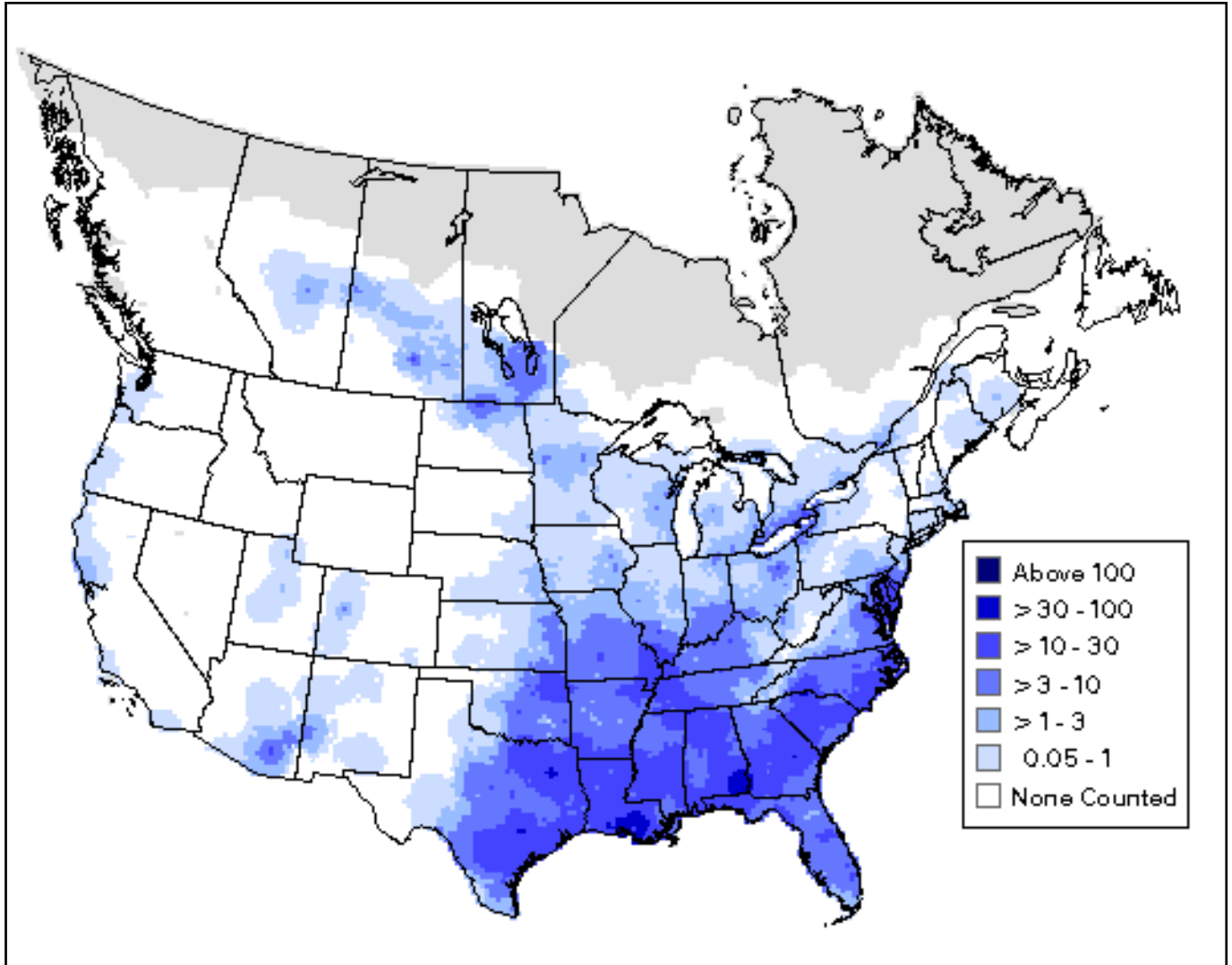
Figure 7. Mean annual number of purple martins observed on Breeding Bird Surveys during the years 1980 to 1996.

migration occurs in April (**Table 4**). Montane populations in Colorado arrive later, with most individuals arriving in late April (Bent 1942) to May (Andrews and Righter 1992). Martins begin to form post-breeding flocks soon after the young fledge, remaining together through fall migration (Brown 1997). Such pre-migratory flocks are sometimes enormous in the eastern United States (e.g., >100,000 birds at sites in Missouri, Louisiana, and South Carolina; citations in Brown 1997). Great Plains and Rocky Mountain populations appear to begin their southward migrations in August (e.g., a migratory flock was seen in late August at Overland Reservoir, Delta County Colorado; Reynolds et al. 2002), and most birds are gone by late September (**Table 4**). Although the exact migratory routes of purple martins are not well known, large numbers (of presumably *Progne subis subis*) pass through the Gulf of Mexico lowlands in eastern Mexico in August. Southwestern *P. s. hesperia* were noted departing

the Tucson, Arizona area from 23 September to 4 October (Cater 1944). There is no information available on the migratory pathway used by montane *P. s. arboricola*. Phillips (1986) suggested that the majority of purple martins migrate along the Mexican coastline, apparently avoiding the central highlands.

During the breeding season, martins appear to forage solitarily or in pairs and may forage far from their nest site (Brown 1997). Birds from late-summer roosts may range up to 100 km during daily foraging trips (Brown and Wolfe 1978, Russell and Gauthreaux 1999). Purple martins do not forage during periods of heavy rain or when the temperature is less than 9 °C (Brown 1976).

Purple martin populations on the Great Plains are likely to be highly linked due to the relatively strong

Table 4. Timing of purple martin spring arrival and fall departure dates within USDA Forest Service Region 2.

Area	Spring arrival date	Fall departure date	Source
South Dakota	late March (earliest)	late August to October	Tallman et al. 2002
Wyoming*	May	early August	Dorn and Dorn 1999
Nebraska	March (early) to late April (peak)	late August (peak) to early October	Sharpe at. 2001
Colorado	April to May	September	Andrews and Righter 1992
Kansas	March (early) to April (peak)	August (peak) to late September	Thompson and Ely 1992

*Wyoming records represent presumed migrants.

dispersal tendencies of first year breeders (Allen and Nice 1952, Brown 1997). Only a small percentage (1 to 5 percent) of fledglings return to their natal colony to breed (Hicks 1933, Brown 1997), with some first-year birds nesting more than 300 km from their natal sites (Allen and Nice 1952). In addition, some adults have been shown to disperse relatively large distances from the previous year's breeding site (Brown 1997). There are no data on dispersal tendencies of the *hesperia* or *arboricola* subspecies. Given the large geographic distance between *arboricola* and *subis* populations, as well as the marked differences in ecology between the two subspecies, there is likely no genetic interchange between them.

Habitat

Nesting habitat

In eastern North America, purple martins historically nested along forest edges and clearings, especially near areas of water (Brown 1997, Ducey 2000). Nest sites included holes in trees as well as niches on cliffs. Early reports of purple martins nesting in Nebraska (prior to colonization by Europeans) suggested that they largely bred along river valleys, utilizing holes in cottonwoods (*Populus* spp.) and other trees, as well as niches on cliffs (Ducey 2000). However, at some point in the past 300 years, eastern martin populations began nesting in man-made structures and are now restricted to breeding in martin houses, gourds (erected by humans), holes in buildings, or niches in traffic lights and street lamps (Brown 1997). Early reports suggest that eastern martin populations began their nest-site shift before European colonization; Catesby (1731) noted martins utilizing hollowed-out gourds erected by Native Americans in the southeastern United States in the early 1700s.

Interestingly, the same pattern of nest-site shift occurred in another eastern hole-nesting species, the chimney swift (*Chaetura pelagica*). This species also formerly bred in holes in trees and natural niches but is now mainly restricted to nesting in man-made structures.

Similar to purple martins, chimney swifts have a closely-related western sister species, Vaux's swift (*C. vauxi*) that has retained the habit of nesting in natural holes. The reasons for the shift in nest-site preference among eastern purple martin populations are not entirely clear, but Hill (1992a) cited several references to Native Americans hanging hollowed-out gourds for martins, and if widespread, this custom may have resulted in the nest-site shift. The potential factors favoring a shift in nest-site choice include avoidance of interspecific competition for nest holes, avoidance of nest parasites, predator avoidance, and benefits derived from nesting in loose colonies. Unfortunately, testing such hypotheses (with comparative analyses) is not currently possible as eastern purple martins nest in natural sites only on rare occasions (e.g., Simpson 1993).

Currently, purple martins on the Great Plains appear to be restricted to breeding in man-made structures, especially martin houses and gourds. As a consequence, they are typically found breeding in open suburban or rural (e.g., farmyard) habitats where landowners erect specially constructed martin "apartments" or small groups of gourds. This includes all of the martins breeding in Kansas, Nebraska, and South Dakota. There are historical references to purple martins in the Black Hills of South Dakota, with observations of "families" of martins roosting in dead pines (Grinnell 1875, Visher 1909). Thus, it is likely that purple martins formerly bred in natural nest sites in suitable areas of the Black Hills, as they did along forested river bottoms in Nebraska (Ducey 2000).

In the Rocky Mountains, the *arboricola* subspecies breeds in mid-elevation (2000 to 3000 m; 6600 to 9900 ft.) forest edges, typically near areas of open water (Gillihan and Levad 2002, Reynolds et al. 2002). Reynolds et al. (2002) made a detailed study of the nesting habitat of purple martins in west-central Colorado and characterized martin nesting habitat as mature (>60 years old) aspen stands on gentle slopes adjacent to large forest openings. The majority of nests were also within 300 m of water (e.g., streams, ponds), a factor that has also been noted as important (but not

critical) to eastern *subis* populations (Jackson and Tate 1974). Nests were placed in old woodpecker holes in aspens that averaged 21 m (69 ft.) in height and 37.5 cm (15 in.) diameter at breast height (dbh). Nest holes averaged 7.7 m (25.5 ft.) from the ground to the bottom on the entrance, and they were oriented towards nearby forest openings. In these situations, martins tended to nest solitarily, but on several occasions two to four pairs nested within the same aspen stand, within 100 m (330 ft.) of each other.

It is important to note that in some areas of the southwestern United States, purple martins nest in cliffs (Morton cited in Brown 1997, B. Stutchbury personal 2004), and this potential nesting habitat should be investigated in Region 2.

As summarized in the Colorado PIF Landbird Conservation program (www.rmbo.org/pif/bcp/phy62/ aspen/puma.htm), key habitat elements for purple martins in Colorado include:

- ❖ live aspen trees with a dbh of at least 14 inches

- ❖ nest trees located within 175 feet of open parks/meadows

- ❖ nest trees located within 1000 feet of standing water

These habitat elements were also highlighted in recent studies by Gillihan and Levad (2002), based upon measurements taken at 81 purple martin nest sites throughout western Colorado. Their representation of a typical purple martin nest site landscape is depicted in **Figure 8**. The average elevation of martin nesting sites in Gillihan and Levad's study was 8866 ft. (range 7900 to 9840 ft.), but the authors cautioned that elevation *per se* was not an important factor in nest site selection. Gillihan and Levad (2002) also stressed the importance of live trees versus snags as purple martin nest sites. In their study, 71 of 80 martin nests were located in live trees. This differs markedly from the situation in Oregon (Horvath 2000) where conifer snags are the preferred nest sites. The difference was attributed to the relatively short "lifespan" of aspen snags, especially at forest edges where wind accelerates snag fall.

To the west of Region 2 in Utah, purple martins also breed in high elevation forests, and, at least historically, at lower elevations in buildings in towns (e.g., Vernal; Twomey 1942, Woodbury et al. 1949). In New Mexico and Arizona, montane populations

breed from 2000 to 2800 m (6600 to 9240 ft.) in most of the high elevation forests, preferring to use old woodpecker holes in dead pines (Ligon 1961, Phillips et al. 1964). Montane purple martins in Sonora, Mexico (presumably also *arboricola*), also breed in high elevation pine forests (Russell and Monson 1998). Purple martins breeding along the coast from California to southern British Columbia also utilize old woodpecker holes. In Monterey County, California, nests located during recent breeding bird atlas work were located from sea level to 1400 m (4620 ft.) and were placed in cavities in dead ponderosa pines, live sycamores, and under highway bridges (Roberson and Tenney 1993). In Oregon, purple martins typically nested in dead Jeffrey pine (*Pinus jeffreyi*) or spruce, but also in building crevices and more recently in nest boxes and under bridges (Gabrielson and Jewitt 1940, Marshall et al. 2003). A recent study by Horvath (2000) in Oregon found that purple martins nested primarily over water, in nest boxes, gourds, pilings, and snags. In rural areas in Washington, martins nest at low-elevation coastal sites, utilizing wood pilings over water and occasionally holes in trees (Smith et al. 1997). Similar sites are used in south coastal British Columbia, but next boxes have become an increasingly important resource there and are apparently responsible for maintaining local populations of martins (Campbell et al. 1997). From southern Arizona southward, purple martins (the *hesperia* subspecies) nest in deserts at low elevation in saguaro cactus (*Carnegiea gigantean*) (Monson and Phillips 1981), in rock cliffs on Gulf of California islands (Banks and Orr 1965), and in sandstone washes in Baja California (Bancroft 1930).

Foraging habitat

Historically, purple martins breeding in eastern North America were thought to forage around their nesting sites, which included forest edges and riparian areas, wooded ponds, and beaver marshes (Brown 1997). The situation in eastern North America today is very different. Although martin foraging habitat still appears to depend on the locality of suitable nesting sites, such sites are now typically suburban areas or even heavily populated cities. Purple martins (the *hesperia* subspecies) in the desert Southwest may feed far from their nesting sites over habitat in which they do not nest (Phillips et al. 1964, Brown 1997). In the Rocky Mountains, the *arboricola* subspecies forages over open mountain meadows, lakes, and beaver ponds (Hayward et al. 1976, Gillihan and Levad 2002), but there are no data available on the foraging range of individuals from their nest sites.
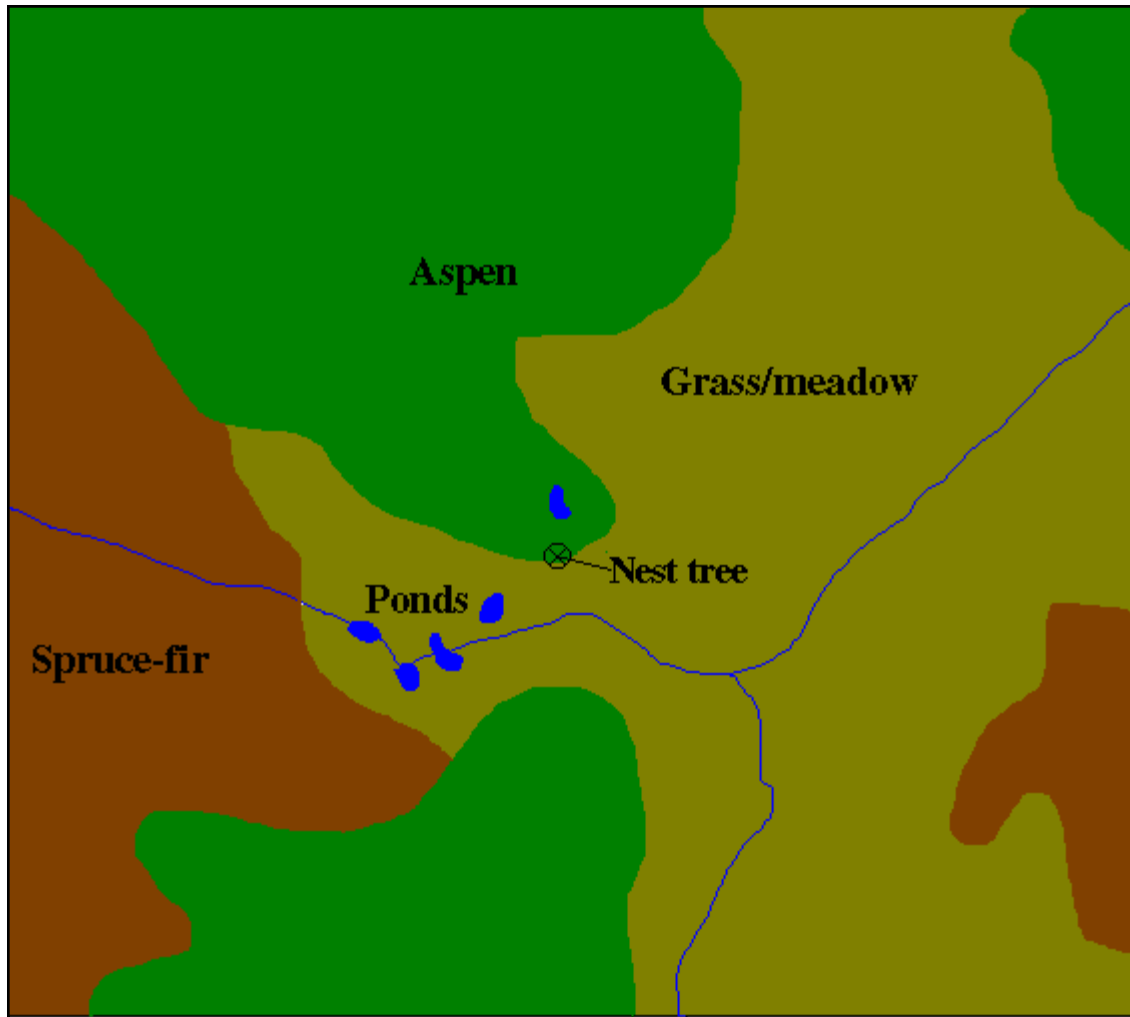
Figure 8. A representation of the typical landscape features surrounding purple martin nest sites in western Colorado. Note that the key habitat elements are edge habitat along a mature aspen stand, and proximity to open water and grassy meadows. The figure was redrawn from Gillihan and Levad (2002).

In the eastern portions of their range, purple martins still appear to prefer nesting near open water, but they will colonize areas far from available water sources. Montane and northwestern coast populations apparently depend on nest sites near water. In Colorado, most nest sites are located within a few hundred meters of open water (e.g., beaver ponds; Levad 2003). The attraction to areas of open water may relate to a number of factors: 1) the presence of submerged, dead trees with nesting holes (historically important in eastern populations; likely still important in Rocky Mountain and northwestern populations), 2) a reliable source of insect prey such as dragonflies and damselflies (Odonata), as well as ephemeral blooms of aquatic insects (e.g., Chironomidae), and 3) importance as a foraging area early in the season or at high altitudes, when cold temperatures often drive martins to feed low over the water (Riggs 1947, Brown 1997). During cold

weather, eastern martins (*subis* subspecies) will also feed at low altitudes in cities, apparently attracted to the warm microclimate that attracts insects (Robins 1971, Brown 1997).

The only quantitative study of purple martin foraging behavior was carried out in Illinois by Graber et al. (1972). They classified field types in their rural study area and found that in descending order, martins preferred to forage over fallow fields, shrubby areas, oat fields, soybean fields, alfalfa fields, and cornfields.

Food habits

Purple martins feed primarily on flying insects, apparently taking advantage of those prey that are most easily available. Compared to most other swallow species, martins feed at relatively high altitudes (50 to

150 m), moving to relatively low altitudes and closer to their nest sites later in the day (Brown 1997). During the breeding season, the pair often feeds together; Brown (1997) suggests this may simply represent mate-guarding by male martins. There is conflicting opinion as to whether breeding martins feed in groups (Johnston and Hardy 1962, Brown 1997), but observations of such behavior may relate to incidences of martins converging on blooms of ephemeral insects. Early and late in the breeding cycle, martins spend long periods away from the nest foraging. Once egg laying has begun, they tend to make much shorter foraging trips and spend more time in the immediate nest area (Brown 1997).

Detailed studies of food preferences are only available from two areas: Kansas and Alberta. In Kansas, Johnston (1967) made a detailed study of martin food habits over the course of the breeding season and found representatives of 57 insect families, predominately Coleopterans (Scarabidae, Curculionidae and Carabidae), Homopterans (Aphidae), Hemipterans (Corimelaenidae), Hymenopterans (Ichneumonidae) and Dipterans (Tipulidae). The diet varied according to the time of the season, with dipterans and homopterans important earlier in the season, and hemipterans, lepidopterans, and lepidopterans more prevalent later in the season. In the aspen-parkland region of Alberta, Walsh (1978) collected prey brought to martin nestlings and found a total of 14 insect families, the most common of which were Odonates (Aeshnidae, Libellulidae, and Coenagrionidae), Dipterans (Syrphidae and Chironomidae), Lepidopterans (Nymphalidae), Hymenopterans (Siricidae and Formicidae), and Coleopterans (Cerambycidae). A range-wide study of martin foods (Beal 1918) found 23 percent Hymenoptera, 16 percent Diptera, 15 percent Odonata, 12.5 percent Coleoptera, and 9.4 percent Lepidoptera.

Martins may concentrate their foraging efforts on local emergences of termites and mayflies (Brown 1997). Although flying insects comprise the bulk of the diet, martins are known to occasionally take some terrestrial prey including caterpillars (Brown 1997). The oft-cited notion that purple martins are prodigious mosquito predators has no basis in fact (Kale 1968).

Breeding biology

As with other aspects of the biology of purple martins, the following accounts are based largely on studies in eastern North America. While the overall patterns are likely similar for western, montane populations (*Progne subis arboricola*), there may be subtle differences due to both the local environment and social situations (strongly vs. loosely colonial). Differences between *subis*, *arboricola* and *hesperia* subspecies are noted when they are known.

Courtship, pair formation and nest-site selection

On rare occasions, male and female purple martins are already paired when they arrive at the nest site. More typically, males defend potential nest sites early in the spring and advertise to arriving females through a flight display (Johnston and Hardy 1962). Pair bonds form quickly, and once paired, some males (especially first-year birds) mate-guard their female extensively, following her whenever she leaves the colony area. In other cases, including the Southwest desert *hesperia* subspecies, males rarely guard their mates (Morton 1987, Stutchbury 1991a). As Brown (1997) notes, such variance in mate-guarding behavior (both within and among populations) is rare among swallows, where mate-guarding is typically an all-or-none behavior.

Although purple martins are typically monogamous, polygyny has been observed in eastern (*subis*) and southwestern (*hesperia*) populations; this may explain the prevalence of mate guarding. In such cases, males provide more care to the first female (and her brood) and will typically abandon the second female if challenged by a rival male. In highly social, eastern populations, there may be a considerable amount of extra-pair paternity (Morton 1987, Morton et al. 1990, Wagner et al. 1996a, Wagner et al. 1996b). Extra-pair copulations typically take place between neighbors, and older males are more likely to sire offspring via such behavior. The role of the female in initiating extra-pair copulations remains unclear (for differing views, see Brown 1978a and Wagner et al. 1996a).

Individual females or paired birds typically inspect several potential nesting sites before settling. Females apparently choose nest sites based largely on site characteristics, rather than male quality (Johnston and Hardy 1962, Brown 1997). In southeastern United States populations, hollow gourds have been utilized since at least 1712, and these are apparently preferred over traditional martin "apartments" (Brown 1997). However, the majority of purple martins nesting in the eastern United States and Canada now utilize human-supplied martin houses, typically consisting of eight to 12 rooms, or gourds (Jackson and Tate 1974, J. Hill III personal communication 2004). A wide variety of other nest sites have been reported (see summary in Brown 1997), including crevices in buildings, holes in traffic lights, and crevices in piers and docks (the latter are especially important in Pacific Coast populations). The

arboricola subspecies in the Rocky Mountains typically nests in old woodpecker holes, often in live aspens (Gillihan and Levad 2002, Levad 2003). In Oregon, martins now mainly (75 percent of all 1998 nesting records) utilize man-made structures; however, birds nesting away from the coast often use snags (Horvath 2000). In British Columbia, martins also primarily use man-made structures for nesting (Fraser et al. 1997). The *hesperia* subspecies in Arizona and Mexico utilize live saguaro cacti (Stutchbury 1991a) as well as rock crevices on Gulf of Mexico islands (Banks and Orr 1965) and sandstone cliffs on mainland Baja California (Bancroft 1930).

Nest construction is carried out largely by female martins although males may initiate the nest building and bring green leaves during construction (Brown 1997). Within the chosen nest cavity, martins assemble a loose structure comprised of small twigs, grass, green leaves, and mud (the latter especially around the entrance hole). The function of green leaves is not known (Hill 1989), but they are primarily added to the nest by the male during the incubation period (B. Stutchbury personal communication 2004).

Clutch and brood size

Clutch size is typically four or five eggs (mean = 5.4), with a normal range of three to six (Brown 1997) and with seven-egg clutches occasionally reported (Hill 1999). **Table 5** gives clutch sizes and brood size at fledging reported from studies across North America. Surprisingly, within the range of the eastern *subis* subspecies, there is no apparent latitudinal increase in clutch size, a common pattern in most passerine birds (Lack 1968). Because old birds typically nest early and lay slightly larger clutches than young birds, clutch size declines over the course of the breeding season (Finlay 1971, Brown 1978b). Differences in clutch size between martin pairs with first-year and older males

averaged 4.29 vs. 5.00 in Alberta (Finley 1971), 4.11 vs. 4.97 in Texas (Brown 1978b), and 4.19 vs. 4.90 in Pennsylvania (Hill 1997a), respectively. All eggs within the clutch typically hatch over a period of 48 hours.

Analysis of DNA from one purple martin colony in Maryland suggested that, among first-year breeders, about one third of all young being raised were the result of intraspecific brood parasitism. In the same area, Morton et al. (1990) showed that there may be a substantial number of extra-pair fertilizations within colonies, with females preferentially mating with older males. It is not yet known whether similar parasitism and copulatory behavior are prevalent in western populations, but given the dispersed nature of nest sites in the West, they are probably rare there

Parental care and offspring behavior

Both parents incubate the eggs, but females perform the vast majority of the incubation duties (Brown 1997, and only they develop a brood patch (Hill 1993). The incubation period lasts 15 to 18 days (Hill 1997b). During this time, females incubate 70 to 75 percent of daylight hours, with lengths of incubation bouts depending on the local weather conditions (Allen and Nice 1952, Brown 1997). The young are brooded by only the female and extensively at hatching. The frequency of brooding decreases as the young age until it finally ceases when they are approximately 10 days old (Allen and Nice 1952).

Nestlings are fed by both parents, with increasing frequency from hatching until they are 17 to 21 days old. Females make more feeding visits than do males, providing 56 percent of the food deliveries to broods in Missouri (Widmann 1922) and Arizona (Stutchbury 1991a). In general, parents deliver food to broods approximately 13 times per hour, depending on the stage of the nestling cycle (Widmann 1922, Brown

Table 5. Clutch size and fledging success of purple martins in North America.

Study area	Clutch size (mean)	Fledging success	Citation
Kansas	4.2	—	Johnston 1964
Missouri	4.9	2.4	Widmann 1922
Alberta	4.8	3.4	Finlay 1971
British Columbia	4.6	—	Fraser et al. 1997
Texas	4.6	4.2 (adults), 3.8 (first-year)	Brown 1978b
Michigan	4.9	3.0 and 1.2 (different years)	Allen and Nice 1952
Maryland	4.0	—	Klimkiewicz in Brown 1997
Arizona	3.9	—	Stutchbury 1991a

1997) and brood size (Kamp 2000). Parents continue to feed fledged juveniles, at least until four or five days post-fledging, and young appear to become independent of adults seven to 10 days after fledging (Brown 1997).

Nestling growth

Young purple martins grow quickly, nearly doubling their weight every three days between ages three and nine days, and peaking at about 60 grams at 17 to 21 days of age (Allen and Nice 1952, Hill 1994a). At that point, they slowly begin to lose mass, declining to 50 grams around fledging age (26 to 31 days of age). Feathers begin external development when the young are about 12 days old, and the flight feathers continue to grow throughout the nestling stage (Brown 1997), and likely for several weeks thereafter.

Timing of breeding and breeding success

Table 6 provides a summary of the timing of major reproductive events of purple martins in Region 2 states. Martins at lower latitudes and lower altitudes generally begin breeding earliest. Purple martins are largely single-brooded, with cases of double-brooding being rare and apparently only known with certainty from the southern United States (Brown 1997). Nonetheless, such double-brooding can lead to significantly greater annual reproductive success (in Texas, 8.3 vs. 4.2 young per year, for double- and single-brooded females, respectively; Brown 1997).

Reproductive success varies among years and often depends on the local weather conditions, with poor success typical during cold, wet years (Allen and Nice 1952, Hill 1997c). First time breeders generally realize lower reproductive success than older birds, largely as a result of laying smaller clutches (Brown 1997). **Table 5** summarizes the number of fledglings per brood from various areas in North America.

Demography

Genetic characteristics and concerns

Purple martins are widely distributed in eastern North America. Although many adults are known to return to the same breeding colonies in subsequent years, Brown (1997) suggests that adult dispersal is poorly understood, and there are some observations of extensive between-year movements between nesting sites (e.g., Hicks 1933). Natal philopatry is weak, with reported return rates of banded nestlings averaging 5 percent (n = 20) in Ohio (Hicks 1933) and 1 percent (n = 203) in Texas (Brown 1997). The majority (79 percent) of these returning nestlings are apparently males (Brown 1997). That first-year martins may disperse large distances from their natal colony is supported by data from Michigan, where Allen and Nice (1952) found that 6.4 percent of banded nestlings that were later recaptured were breeding at least 100 miles from their natal sites. However, in Pennsylvania, Hill (2003) found that 96 percent of 84 color-banded adult and sub-adult purple martins observed at a colony over a 9-year period were breeding within 37 miles of where they hatched. Thus, adult and natal dispersal, together with a contiguous distribution in eastern North America, suggests that gene flow is likely high among purple martin populations. The situation in western North America is much less clear. Populations in the Rocky Mountains are patchily distributed, and the extent to which these populations are linked genetically will remain unknown until banding studies have been carried out in these areas.

Life history characteristics

Both male and female purple martins typically breed first as one-year olds. Within many populations of purple martins, an unknown proportion of birds are "floaters" that forgo breeding. These birds are typically

Table 6. The approximate timing of major breeding events for purple martins in USDA Forest Service Region 2.

Study area	1st clutch date	Hatch date	Fledge date	Citation
Kansas	early June	late June	July	Johnston 1964
Colorado	late May, early June	mid June	early July	Levad 1998
Nebraska	late May to early June	mid June	early July	Molhoff 2001
South Dakota[1]	late May, early June	mid June	early July	Peterson 1995

[1] South Dakota phenology data are from a single colony in Gregory county, southcentral Nebraska.

first-year birds (Rohwer and Niles 1977, Stutchbury 1991b, Brown 1997), and although the proportion of floaters is usually unknown, Wagner et al. (1996) reported that 12.9 percent of yearling males went unmated throughout the breeding season. Purple martins are sexually dimorphic and have delayed plumage maturation, with both sexes attaining their adult plumage during their third year (Stutchbury 1991c, Hill 1992b). Brown (1997) suggested that reports of double-brooding in purple martins were usually not credible and that only a small number of birds ever produce two broods in a season (and only in the southern portion of the breeding range). Although reproductive success varies from year to year, depending largely on local weather conditions, purple martins typically realize relatively high reproductive success. Using the SURVIV program, Francis (1995) estimated average survivorship values of 60.9 percent for adult (>1 year old) and 32.2 percent for first-year (= 1 year old) purple martins. A robust estimate of juvenile survival, from fledging to the following breeding season, has remained difficult to obtain as purple martins exhibit low natal philopatry.

Analysis of life-cycle diagrams and their associated demographic matrices is problematical given the difficulty in estimating some of the key life history data for purple martins. The analysis in **Appendix A** uses demographic data from studies on the *hesperia* subspecies in Arizona (Stutchbury 1991a), the summary in Brown (1997), as well as survival data from Francis' (1995) demographic analyses. At the simplest level, the modeling suggests that purple martin population growth is more sensitive to variation in survival rates than to variation in reproductive rates. More detailed analyses suggest that the survival of adults (relative to first-year martins) may be the primary factor affecting purple martin population dynamics. Although reproductive success and the survival of first-year birds are important factors, the survival of adults appears to be the critical demographic trait buffering populations against environmental uncertainty. It is important to note here, however, that juvenile survival rates have proven difficult to measure. Obtaining better estimates of juvenile and adult survival rates is clearly a primary information need for purple martins in Region 2 (see Information Needs section).

The major conclusions from matrix projection models can be summarized as follows (see **Appendix A** for details):

❖ First-year and adult survival account for 67 percent of total "possible" sensitivity. Any absolute changes in this rate will have major impacts on population dynamics.

❖ First-year and adult survival account for 62 percent of the total elasticity, compared to the total of 38 percent of the elasticities for all the fertility transitions. Proportional changes in early survival will have a major impact on population dynamics. The elasticities place a greater emphasis on the importance of adult survival than do the sensitivities (37 percent vs. 30 percent).

❖ Similar conclusions from the sensitivity and elasticity analyses suggest that survival rates are critical to the population dynamics of purple martin.

❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of variation in survival to population dynamics. Management should consider that dispersal options for young individuals and over-winter survival of all age-classes may be critical to purple martin populations.

Social patterns and spacing

Purple martins are highly social and breed colonially, at least in the eastern portions of the range. Consequently, there is little classical territorial behavior other than adults defending specific nest sites from potential intruders. Adults breeding in saguaro in Arizona defend "territories", usually an area of 20 to 30 m around their nest sites. The dispersion of nest holes in these areas means that adult males may defend nest sites up to 115 m apart (Stutchbury 1991a, Brown 1997). In both eastern and western populations, purple martins gather in large flocks prior to migration. These flocks can be enormous (>50,000 birds) in the eastern United States.

Colony size in the eastern portions of the range depends on the number of the nesting cavities available. In human-supplied structures, colony size is typically less than 12 pairs, but much larger colonies can form at sites with large martin "apartments" (Brown 1997). Eastern *subis* pairs still occasionally nest solitarily, but such behavior is rare (see references in Brown 1997). Arizona *hesperia* martins typically breed solitarily, with at least 100 m between neighboring nest sites (Stutchbury 1991a). The *arboricola* subspecies appears to be somewhat more colonial, as recent survey work

in Colorado has found several instances of single trees containing more than one nesting martin pair (Gillihan and Levad 2002), with an average of three pairs per colony stand (range 1 to 10 pairs; Levad 2003). One presumed *arboricola* colony in a sandstone cliff near Flagstaff, Arizona contained more than 100 pairs of martins (Morton in Brown 1997).

Factors limiting population growth

The vastly different nesting ecologies of the western and eastern subspecies of purple martins mean that the factors limiting population growth are likely very different in the two areas. In the eastern portion of the range, including the Great Plains, access to high-quality, human-supplied housing is an important factor limiting population growth. In western Colorado, nest site availability also appears to be the key to local population growth. Martins prefer live, large aspens, a resource that has not been traditionally seen as important to wildlife in western forests. Currently, there is little understanding about how this resource fluctuates in space and time in Region 2. Oddly, there is apparently suitable aspen habitat further east in Colorado that is not utilized by martins (**Figure 6**). The lack of martins in those areas may be linked to the fact that western slope aspen is a climax community, a situation that does not exist further east. Consequently, large, live aspen are likely much more available on the western slope. In any case, habitat choice in the *arboricola* subspecies is still not yet fully understood.

Across the martin's range in North America, the biggest factor limiting population growth is probably competition for nest sites, especially with European starlings. Starlings have taken over historic breeding areas in coastal Oregon (Horvath 2000). Similar problems exist in eastern North America, although the problem there is mitigated somewhat by the abundance of human-provided nesting sites and the fact that eastern martins nest in relatively large colonies. Recent survey work in the aspen forests of western Colorado have failed to document nesting starlings, but given the relatively small martin population there (total Colorado population 500 to 1000 birds; Gillihan and Levad 2002), continued monitoring has been suggested (Gillihan and Levad 2002).

Community ecology

Figure 9 presents a graphical representation of the interaction of purple martins with predators and competitors, and how these factors may affect habitat use. Adult and free-flying martin young are preyed upon by a number of avian predators including various species of hawks and owls, Mississippi kites (*Ictinia mississippiensis*), merlins (*Falco columbarius*), and even great blue herons (*Ardea herodias*). Bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), squirrels (*Sciurus* spp.), and several species of snakes may also prey on adults (usually caught in the nest at night) or on eggs (see references in Brown 1997). Another source of adult, nestling, and egg mortality arises out of competition for nest holes (see below), whereby house sparrows and European starlings may kill adults and nestlings, and remove eggs (Brown 1977).

Interspecific competition with other hole-nesting bird species has been extensively cited as a problem for local populations of martins. In eastern areas populated by the *subis* subspecies, this form of competition is now largely between martins and introduced house sparrows and European starlings for access to nest holes. These two species may occupy martin nest sites prior to the return of martins in the spring. In addition, they may usurp martins from nest sites later in the season, not only causing reproductive failure, but occasionally killing adults (Brown 1977). Although the extent to which interspecific competition plays a role in regulating mountain *arboricola* populations is unknown, the list of potential competitors for nest holes in aspen forests includes a number of common native species including tree swallows (*Tachycineta bicolor*), violet-green swallows (*T. thalassina*), house wrens (*Troglodytes aedon*), and mountain bluebirds (*Sialia currucoides*). Starlings were not observed nesting in western Colorado aspen stands in any of the three years of surveys (Gillihan and Levad 2002). In coastal Oregon populations, purple martins have abandoned some traditional nesting sites due to competition with European starlings (Horvath 2000). In the desert Southwest, purple martins compete for nest holes with common flickers (*Colaptes auratus*), Gila woodpeckers (*Melanerpes uropygialis*), and brown-crested flycatchers (*Myiarchus tyrannulus*; Stutchbury 1991a). Martins (presumably *arboricola*) breeding in the Chiricahua Mountains of southeastern Arizona engaged in chases with common flickers and acorn woodpeckers (*Melanerpes formicivorus*) around potential nest sites.

The ecto- and endoparasites of purple martins have been relatively well-studied. Martins are host to an extensive list of ectoparasites including cimicid bugs, ticks, fleas, dipterans, dermestid beetles, lice, and mites. In western populations (*hesperia* and *arboricola* subspecies), the most prevalent ectoparasites are the cimicid bugs (*Hesperocimex sonorensis*, Sonora; *H. cochimiensis*, Baja California; *H. coloradensis*,

WEB			CENTRUM
4	3	2	1

RESOURCES

water and soil — disturbance (fire, logging)— large, live aspen trees —————— primary cavity nesters ————— nest cavities
(e.g., flickers, sapsuckers)

open, grassland habitat
water and soil ———————— disturbance (fire, logging) large, live aspen trees ————— nesting habitat

water and soil ———————— disturbance (fire, logging) —— open, grassland habitat

water ————————— food: flying insects
open, standing water
weather —————————

MALENTITIES

water and soil ——————— large, live aspen trees ———————— nest site competitors: secondary cavity nesters
(e.g., tree swallows, violet-green swallows, house wrens)

proximity to human settlements ——— exotic nest site competitors: secondary cavity nesters
(European starlings, house sparrows)

large, live aspen trees ——————— logging ————————— habitat loss: direct loss of nesting substrate
water and soil
open, grassy habitat ——————— fire suppression ——————— habitat loss: conifer encroachment in montane meadows

open, grassy habitat ————— fire suppression ————————— conifer encroachment ——————— reduced foraging habitat
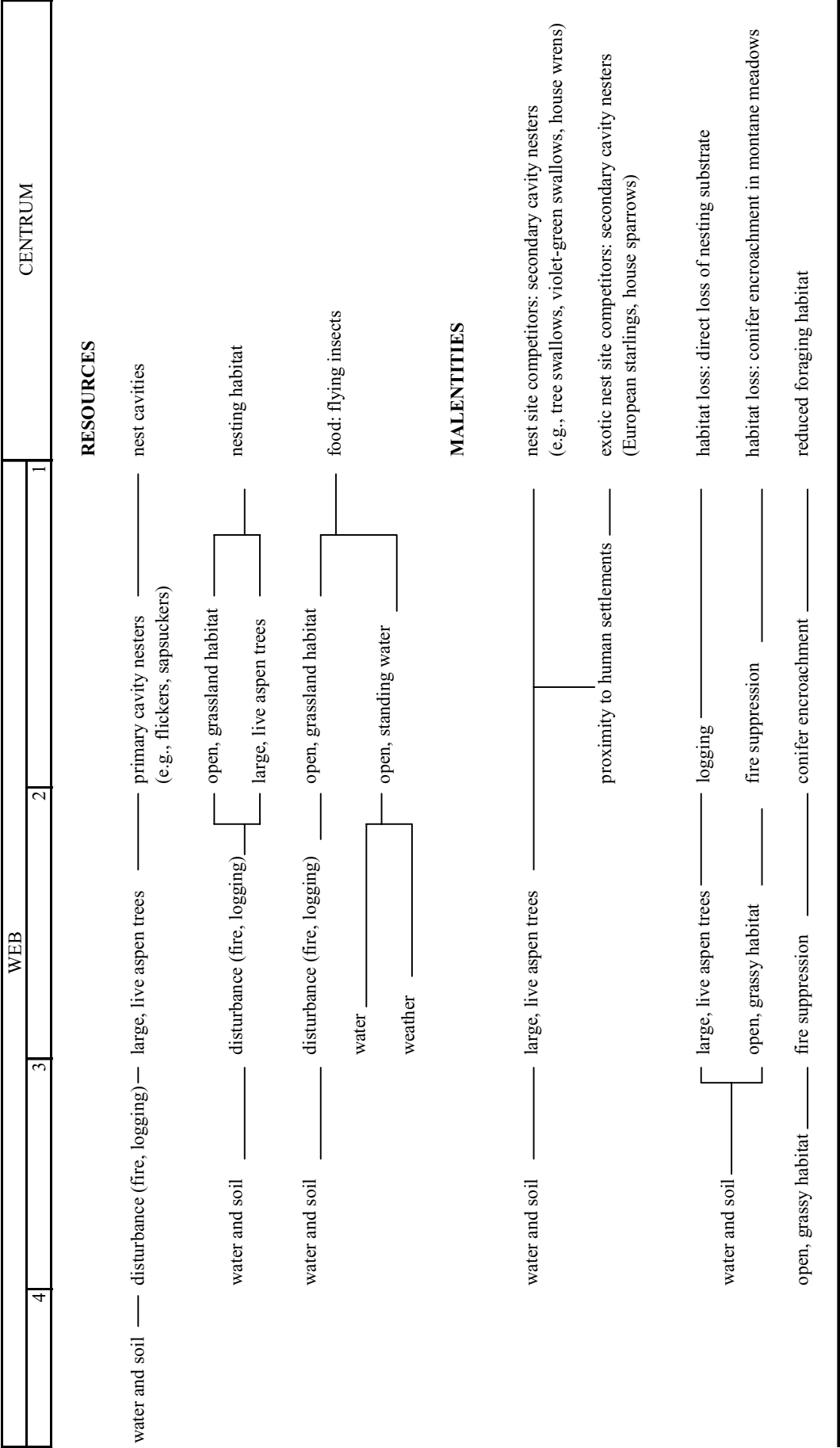
Figure 9. Envirogram representing the web of linkages between purple martins and the Rocky Mountain ecosystem in which they occur. This figure focuses on the *arboricola* subspecies breeding in the Rocky Mountain Region.

Colorado and California; Usinger 1966, Loye and Regan 1991), the flea (*Ceratophyllus idius*, Hill 1994b), and the blowfly (*Protocalliphora hirundo*, Sabrosky et al. 1989). In some martin nests, mites (Dermanyssidae) can number in the thousands and have serious consequences for both adults (e.g., reduced clutch size) and nestlings (e.g., reduced mass and mortality; Moss and Camin 1970). Hill (1994c) found that martin fledging success in parasite-free martin houses was nearly double that of nests in infected houses. Reported endoparasites include nematodes, trematodes, and protozoans (*Haemoproteus prognei*, *Leucocytozoon* spp., *Trypanosoma avium*). In general, there has been little study of the effects of these endoparasites, but *Haemoproteus* are known to cause significant mortality among first year martins (Davidar and Morton 1993).

CONSERVATION

Threats

Threats to purple martins differ regionally. In the eastern portion of the species' range, the primary threat appears to be competition over nests sites from European starlings and house sparrows. Both of these species can take over martin houses, kill adults and young, and remove eggs from nests (Brown 1997). Seyffert (2001) noted a martin colony in northwestern Texas that contained 333 nesting compartments and was occupied by 224 pairs of house sparrows and only 55 pairs of martins. In the Pacific Northwest, where martins still nest in tree cavities, competition from starlings can lead to local extirpation, as has happened in coastal areas of Oregon (Horvath 2000). However, human-supplied martin nest boxes in the Pacific Northwest (and elsewhere) now often incorporate European starling-resistant entrance holes (e.g., Kostka 2001). Competition for nest sites has not yet been noted as a limiting factor for the *arboricola* subspecies in the Rocky Mountain region.

West of the continental divide, where purple martins nest primarily in cavities in mature aspen woodlands, the primary potential threat to population viability is the loss/lack of suitable nesting habitat. Mature aspen groves contain trees large enough to support nesting woodpeckers and sapsuckers that, in turn, provide nest holes for martins.. In addition, aspen colonize openings and are thus located in areas (e.g., near wet meadows) preferred by martins for foraging. Such habitats may be threatened by a number of factors: 1) harvest of mature aspen; 2) lack of aspen stand regeneration, partly due to fire suppression; and 3) water management activities.

Data from recent forest inventories show that the total land cover occupied by aspen ranges widely within Region 2 forests, from 22 percent to less than 1 percent (**Table 7**). Logging of aspen is typically carried out on mature trees, and as mature aspen stands are relatively uncommon in most forests (e.g., 19 percent of the 48,000 acres in the Black Hills; unpublished draft vegetation summaries from Region 2), even small scale logging of mature aspen may pose a potential threat to martin populations. Still, the level of aspen harvest has declined significantly in Region 2 recently (**Figure 10**), suggesting that Region 2 forest managers are actively promoting an increase in aspen coverage.

A more serious threat to purple martins (and other aspen-dependent species) within the Rocky Mountain Region is a lack of aspen regeneration. Aggressive fire-suppression policies appear to have reduced aspen recruitment in (at least) some forests, and represent a threat to future aspen regeneration across the Intermountain West. For example, Romme et al. (1992) found that although aspen stands comprised approximately 15 percent of the total forest cover on the San Juan National Forest in southwestern Colorado, aspen showed relatively poor regeneration, especially at mid-elevations (≈2800 m [9240 ft.]). They predicted a subsequent long-term decline in the overall coverage of aspen on the forest, largely as a result of a lack of disturbance (e.g., fires). In other forests (e.g., Black Hills, Bighorn; see **Table 7**), current levels of aspen cover may be far below historical levels, and this difference may stem from long-term fire-suppression policies. Forest management strategies that incorporate a policy of protection and regeneration of mature aspen stands would benefit not only purple martins, but also other species (e.g., flammulated owl [*Otus flammeolus*], red-naped sapsucker [*Sphyrapicus nuchalis*]) that are also strongly associated with mature aspen stands in some areas.

As purple martins in Region 2 also are strongly associated with open, standing water (e.g., beaver ponds), land management activities that affect hydrological processes may have significant consequences for martin populations. This may include water diversion projects for irrigation, but also less obvious causes of changes in water flow such as road building, timber harvesting, and livestock grazing. Timber harvesting may significantly reduce water retention in mountainous areas by decreasing snow accumulations, increasing runoff, and decreasing water retention. Similarly, livestock grazing in mountainous riparian areas typically leads to increased runoff, increased siltation in streams and ponds, and decreased longevity of ephemeral water

Table 7. Percentage of total land cover occupied by aspen forest, and the total acres of aspen logged during 1999 and 2000 on Region 2 National Forest System lands.

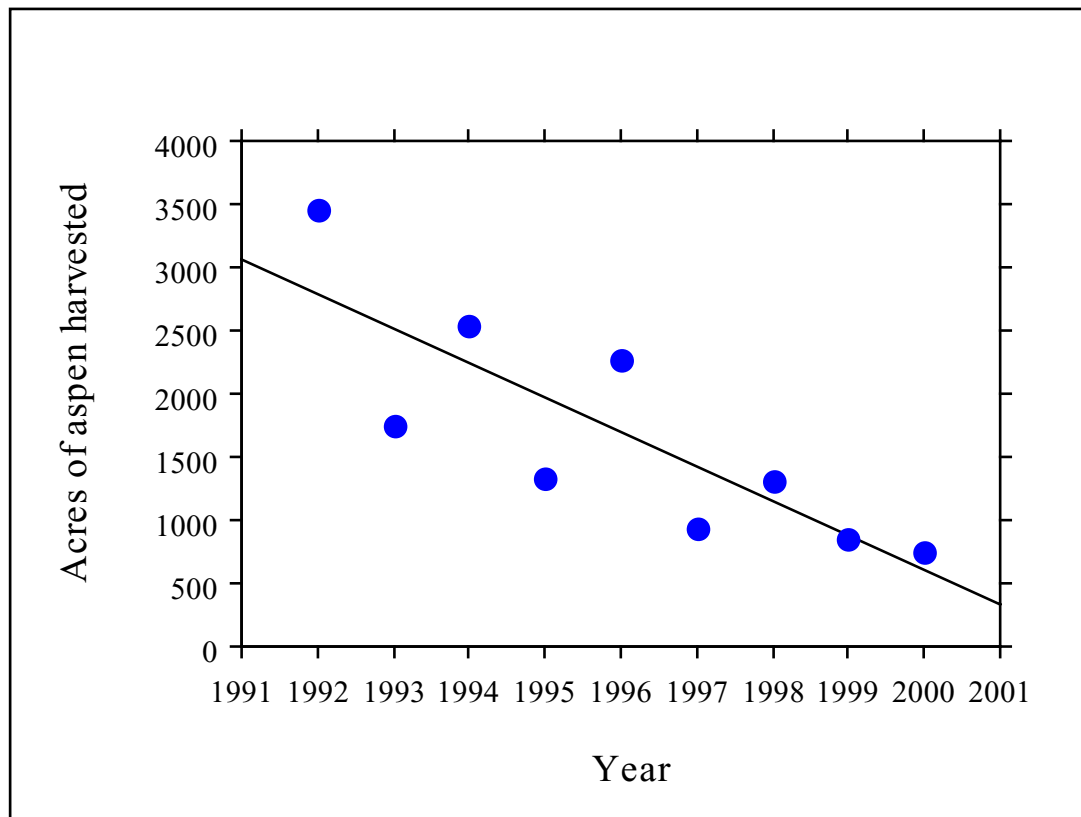| Forest (state)	Acres of aspen	% aspen cover	Acres logged 1999	2000
Bighorn (WY)	10,829	<1	0	0
Black Hills (WY/SD)	48,683	3	210	24
Grand Mesa (CO)	690,058	22	25	130
Medicine Bow (WY)	83,168	6	19	0
Routt (WY/CO)	279,422	21	61	89
Rio Grande (CO)	277,881	1	18	49
Arapaho/Roosevelt (CO)	51,215	3	0	0
Pike/San Isabel (CO)	180,796	7	0	0
San Juan (CO)	307,144	15	103	449
Shoshone (WY)	5,977	<1	0	0
White River (CO)	422,957	17	424	7

Figure 10. The number of acres of aspen harvested on Region 2 National Forest System lands from 1992 to 2000. The negative trend is statistically significant (Spearman Rank Correlation, R_s = - 0.90, P = 0.011).

sources (Kovalchik and Elmore 1992). Alterations in local water flow and retention may lead to decreased insect abundance and thus poor reproductive success by purple martins. Black swift (*Cypseloides niger*) is another species of aerial insectivore that depends on wet, mountainous habitats for foraging areas and may be similarly affected by disturbance to local hydrological patterns (Wiggins 2004).

Brown (1997) noted the potential for pesticide ingestion in purple martins on the wintering grounds in Brazil, but there have been no studies of pesticide accumulations by wintering purple martins. Martins are also susceptible to human interference on the wintering grounds, as they often stage and roost in large flocks within urban areas (Hill 1988). Direct harassment and killing of migrant martins has been noted in Mexico (Morton cited in Brown 1997) and the United States (Bent 1942), but these appear to be isolated, unusual events.

The most commonly noted cause of mortality in purple martins is exposure to adverse weather conditions. This can include local periods of cold, damp weather, during which adult and nestling mortality can be considerable, particularly in the northeastern United States and eastern Canada (Brown 1997). More intense events, such as an Atlantic hurricane in 1972, have led to large-scale mortality of adults and nestlings, and abandonment of breeding areas for many years thereafter (Hall 1972, Tate 1972). Brown (1997) suggested that such weather events represented the greatest source of mortality among purple martins.

Conservation Status of Purple Martins in Region 2

The distribution and abundance of purple martins does not appear to have changed recently in Region 2. Historically, martins appear to have been more common in certain areas, such as the western third of Nebraska and South Dakota. However, the scarcity of martins in those areas today may reflect a shift from nesting primarily in holes in snags in riparian areas, to nesting in man-made structures, largely in and around towns. The status of the species in mountainous areas of Colorado is more difficult to assess. Recent surveying work by the Rocky Mountain Bird Observatory (Gillihan and Levad 2002, Levad 2003) has identified many new martin nesting areas in western Colorado, with the number growing each year as new areas are surveyed. In Wyoming, purple martins have only recently (2004) been found nesting, and only at a single site in the Medicine Bow

National Forest (Faulkner and Levad 2004). Given that purple martins breed in aspen habitat just to the south of the Wyoming-Colorado border, it is likely that martins may be breeding more widely in similar habitat in the south-central portion of Wyoming.

As mentioned in the Threats section, livestock grazing, road building, and timber harvesting may all contribute to degradation of local water quality, decreased or diverted water flow, and a consequent decrease in the abundance of flying insects. Livestock grazing is a common practice on most National Forest System lands in Region 2, and grazing in mountain meadows from May through July may pose a direct threat to martin food supplies while grazing at other times of the year may act to suppress aspen regeneration (Gillihan and Levad 2002). Within each forest unit, open, wet meadows are particularly important as martin foraging areas. Maintaining the integrity (vegetative composition as well as water flow) of existing meadows, as well as creating new wet meadow habitat (e.g., via fire disturbance) would provide long-term habitat sustainability for purple martins.

Regeneration of existing aspen forest has also been noted as a problem within Region 2 (Romme et al. 1992). The variability in the percentage of landcover occupied by aspen forest may be due in part to historical differences in fire suppression within different forests. Maintaining mature stands of aspen typically requires not only protection of existing stands, but also some form of disturbance (e.g., limited timber harvest, fire) and land management strategies that will provide long-term (60 to 90 years) regeneration of mature aspen.

In addition to mature aspen stands and open, wet foraging areas, purple martins also depend on healthy populations of primary cavity constructors such as northern flickers (*Colaptes auritus*), hairy woodpeckers (*Picoides villosus*), and red-naped sapsuckers. Maintaining habitat integrity (e.g., minimizing logging) around mature aspen stands is likely to provide conditions suitable for successful recruitment of these species.

Our current knowledge suggests that only 250 to 500 pairs of purple martins currently breed in Colorado, with a few pairs in southern Wyoming. The extent to which the known breeding areas are linked is unknown, but the species' dispersal abilities suggest that a significant amount of exchange may occur among neighboring populations.

Management of Purple Martins in Region 2

Implications and potential conservation elements

On the Great Plains, martin populations are largely regulated by the availability of man-made nest structures, competition from hole-nesting species, and local weather conditions during reproduction. Consequently, with the exception of erecting and maintaining suitable nesting structures, there appears to be little scope for active management of purple martins on the Great Plains. Montane martin populations appear to be largely regulated by the availability of suitable nesting habitat, but further study is needed to better understand nest-site choice. Currently, aspen is not heavily harvested on National Forest System lands in Region 2 (**Table 7**), but the situation on non-federal lands is unclear. Given the species' apparently strict habitat preferences, it is clear that preserving large, live aspen trees near wet, montane meadows will be critical to maintaining purple martins within Region 2. To date, there is still relatively little known about the breeding biology, life history, and demography of montane populations of purple martins. As a consequence, identifying other potential threats is problematic. In most other areas of the species' range, competition with the European starling for access to nest sites is a serious problem, sometimes leading to the local extirpation of martins (Horvath 2000). The remoteness of most current purple martin nesting areas in Region 2 may explain the lack of starlings in these areas, as starlings typically thrive in and around human settlements.

Based on preliminary results from a three-year study in western Colorado, Gillihan and Levad (2002) made several recommendations for the management of montane populations (*arboricola* subspecies) of purple martins (**Table 2**). The most important of these was for forest management agencies to recognize large, live aspen trees with cavities as a critical resource for purple martins. Traditionally, forest management guidelines recognize snags as important nest trees for martins and other secondary cavity nesting species. However, Gillihan and Levad (2002) found that 71 of 80 purple martin nests in western Colorado were in live trees. They also suggested that current, widespread fire suppression policies within western forests may be negatively affecting purple martins. Fires create ideal conditions for the establishment of new aspen stands, and Gillihan and Levad (2002) suggest that the combination of logging and a lack of replenishing aspen forest due to fire suppression is likely diminishing the availability of climax aspen forest in western Colorado. Finally, these authors also suggested that heavy browsing by elk and cattle is suppressing the maturity of aspen stands, thus preventing the mature stages that purple martins favor. Allowing some small fires to create forest openings, reducing the overall logging pressure on mature aspen in western slope forests, and reducing browsing pressure on young aspen stands are all likely to improve habitat availability for montane populations of purple martins in Region 2.

Although the current level of logging of aspen on Region 2 National Forest System lands is relatively low (**Table 7**), care should be taken to avoid any logging of mature aspen situated adjacent to meadows with areas of open water. This combination of habitat variables represents the prime nesting habitat of purple martins in western Colorado, and as such areas may be limited in occurrence, they should be identified and protected when possible.

Horvath (2000) found that the dependence of Oregon martins on man-made structures appeared to be due, at least partly, to competitive exclusion from natural nest holes by European starlings. In coastal areas, starlings have taken over many of the nest sites historically used by purple martins. Martins breeding inland, however, faced almost no competition from starlings and utilized snags as their primary nesting substrate. These observations suggest that western populations of purple martins should be monitored, with special attention paid to any apparent displacements by European starlings. As mentioned previously, survey work in western Colorado has so far failed to document starlings nesting in mountain aspen stands (Gillihan and Levad 2002).

Tools and practices

In areas where purple martins use man-made nesting structures (e.g., Great Plains), European starlings can be excluded by maintaining an entrance dimension of approximately 31 mm high by 60 mm wide (Horvath 2000). Brown (1997) summarizes the large number of publications on the design and placement of purple martin nest structures. In addition, the Purple Martin Conservation Society (www.purplemartin.com) contains a database of publications and suggestions for construction and maintenance of martin nesting structures. West of the continental divide, where

purple martins nest in tree cavities, monitoring and management is more problematical as data on the species' nesting requirements are still being collected.

Inventory and monitoring

The distribution of purple martins on the Great Plains is well known. In the Rocky Mountains, the distribution of the *arboricola* subspecies has become much better known in recent years, primarily as a result of dedicated martin surveys. Nonetheless, it is likely that the range of *arboricola* in the Rocky Mountains is more extensive than is currently known, and thus further surveys (especially in Wyoming) would be extremely useful in delineating the species' range and habitat requirements. Surveys for existing purple martin colonies/nest sites currently include the following steps:

1. Check available forest inventory maps for the location of aspen groves. Aspen groves in proximity to meadows with open water are particularly attractive to purple martins, but it is equally important to check other areas (e.g., cliffs) in order to gain a better understanding of nest site choice.

2. Visit accessible sites in June and July and watch for the presence of adults flying to and from aspen groves or other potential nesting sites.

3. If possible, attempt to verify whether martins are nesting (i.e., locate trees where martins are entering cavities) or simply using the area for foraging.

4. In particularly suitable areas (open, wet meadows), check any nearby cliff faces for the presence of martins.

Once purple martin nest sites have been located, a monitoring program might include the following (derived from Gillihan and Levad 2002, Levad 2003):

❖ Post each known nesting tree with a "Wildlife Tree" sign, thereby alerting forest managers of the importance of such sites.

❖ Record nest tree characteristics (i.e., tree species, tree height and dbh, height of nest hole above the ground, and the state of the tree [living/decaying/dead]).

❖ Record habitat variables around nesting colonies/nest trees (i.e., proximity of the nest tree to the forest edge, proximity of the nest tree to open water, habitat composition within 200 m of the nest site.

❖ Acquire a GPS reading of nest tree location.

❖ Choose a subset of known colony sites to re-visit each year and count the number of pairs using the site. Such data will provide an important clue to the longevity of sites and may also provide valuable baseline data if land management activities (e.g., logging, water diversion) are occurring nearby.

Management practices

In the Rocky Mountains, land management techniques that would help to sustain or improve the population viability of purple martins include the following:

❖ Improve the regeneration of aspen stands by using prescribed burns, especially in areas adjacent to mid-elevation meadows.

❖ Allow some small-scale fires to burn (i.e., relax fire suppression policy), especially in areas that are near open habitats.

❖ Limit logging of mature aspen groves.

❖ In areas with known martin nesting colonies, limit activities (e.g., logging, road-building) that may affect local water flow.

For land managers in western montane forests, providing adequate stands of mature aspen is the key management practice that will support viable populations of purple martins. However, it is also critical to maintain patches of open, wet meadow habitat as foraging habitat since such sites are strongly preferred by breeding martins (Gillihan and Levad 2002). As mentioned earlier, long-term land management policies (e.g., relaxed fire suppression) that promote aspen regeneration, open habitats, and natural water flow regimes will ensure the sustainability of preferred purple martin habitats.

Gillihan and Levad (2002) suggested that current fire suppression policy in western forests may be having significant negative effects on purple martins because

fire suppression may hinder the establishment of new aspen stands and allow encroachment of conifers onto meadows. They also suggested that current aspen harvesting is outpacing the replacement of stands, and together with fire suppression, is leading to a diminishing nesting habitat for martins. Using prescribed burns, allowing some natural fires to burn (thus creating forest openings), as well as reducing the overall harvest rate of climax aspen forest should maintain or even increase the present level of habitat availability for purple martins.

Information Needs

Purple martins occur in two distinct habitats within Region 2, across the entire central and eastern Great Plains, and also mid-elevation aspen forests along the west slope of the Rocky Mountains in western Colorado (and possibly southern Wyoming). These two populations (subspecies *subis* and *arboricola*) are likely distinct ecologically, with different reproductive ecologies and migratory pathways. Given the tendency for Great Plains populations of martins to nest in and around cities, there is little scope for habitat-based management plans directed at eastern populations. The *arboricola* subspecies, however, is likely very sensitive to management activities in western forests, and thus this section of the assessment will focus on the *arboricola* populations breeding in western Colorado.

While purple martin food habits have been studied in Kansas, there is a clear need for further studies in Colorado as the montane *arboricola* subspecies inhabits different habitats and likely utilizes a very different prey base. Information on the foraging habits and prey of montane martins will provide important baseline data and may help to assess how martins may respond to habitat changes caused by management activities.

Aside from the recent work by Gillihan and Levad (2002) and Levad (2003) on nest site characteristics and population size in western Colorado, there is virtually nothing known about the breeding biology and life history of montane populations of purple martins. A demographic study at one or more of the known nesting sites would help to clarify clutch size, timing of breeding, reproductive success, adult and juvenile survival, philopatry, and other key aspects of the life history of the *arboricola* subspecies. These data are crucial when carrying out population viability analyses, and such analyses cannot be performed until further information is available.

Breeding Bird Survey methodology does not adequately sample the widely scattered and small numbers of montane breeding populations of purple martins. As a consequence, dedicated surveying for new sites (including the possibility of cliff-nesting populations), as well as monitoring of known sites, will be critical to determining any long-term changes in the population status of the *arboricola* subspecies in Colorado (and possibly Wyoming).

It is not clear how forest management practices may be affecting montane purple martin populations in Region 2. Logging of mature aspen may have both negative (destruction of current and potential nest trees) and positive (creation of open habitat surrounding existing aspen stands) effects, depending on local conditions. However, a crucial first step to devising a habitat management plan will be to assess current habitat availability by mapping the location of mature aspen stands. To date, plotting the location of known nesting sites, relative to the location of aspen forests, has not led to a clear relationship between the two (**Figure 6**).

Finally, studies of the relationship between local land management activities (e.g., logging) and purple martin site occupancy and breeding success would help to clarify the effects of such practices on local purple martin populations.

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APPENDIX A

Matrix Model Assessment of the Purple Martin

Life cycle graph and model development

Analyses of life cycle diagrams and associated demographic matrices (McDonald and Caswell 1993, Caswell 2001) can provide valuable insights into which life-history stages may be most critical to population growth. However, constructing models based on incomplete and/or poor quality data may have little relevance (Reed et al. 2002). The following analysis has been constructed using the best available data for purple martins, taken largely from information in Stutchbury (1991a), Francis (1995), and Brown (1997). These data provided the basis for a two-stage life cycle graph (**Figure A1**) and matrix population analysis, for a birth-pulse population with a one-year census interval and a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001) for purple martin.

The model has three kinds of input terms: P_i describing survival rates, m_i describing fertilities, and B_1, describing probability of breeding at the end of the first year (**Table A1**).

$$F_a = P_a * m_a = 0.822$$

$$P_1 = 0.351$$

$$P_a = 0.609$$
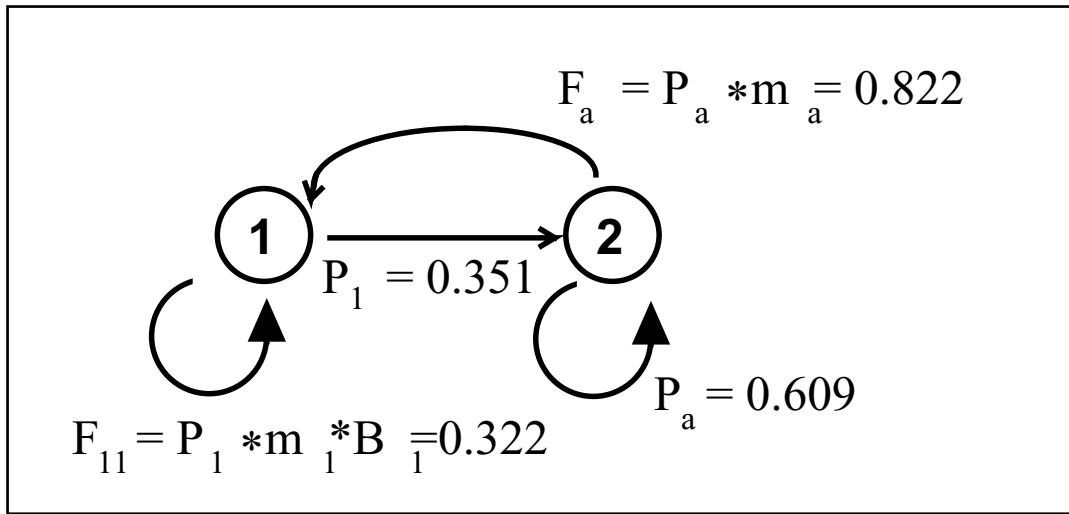
$$F_{11} = P_1 * m_1 * B_1 = 0.322$$

Figure A1. Life cycle graph for purple martin, consisting of circular *nodes*, describing stages in the life cycle and *arcs*, describing the *vital rates* (transitions between stages). The P_i arcs are survival transitions (e.g., first-year survival, P_1=0.351). The leftward self-loop from Node 1 to itself describes the fertility of first-year birds at the end of their first year. The rightward self-loop describes the survival of the mixed-age stage of adult females. The arcs in the life cycle graph have a one-to-one correspondence to the values in the symbolic and numeric values in the cells of the matrices in **Figure A2**.

Table A1. Parameter values for the component terms (P_i, B_i and m_i) that make up the vital rates in the projection matrix for purple martin. Clutch size (females eggs) was estimated as 2.25, with a fledging probability of 0.6.

Parameter	Numeric value	Interpretation
m_1	1.1475	Number of female fledglings produced by a first-year female
m_a	1.35	Number of female offspring produced by an adult female
B_1	0.95	Probability of breeding in the first year
P_1	0.322	First-year survival rate
P_a	0.609	Annual survival rate of "adult" females

The two stages are first-year birds and the "adult" birds. The model therefore assumes that the vital rates of "adults" do not change with age. **Figure A2a** shows the symbolic terms in the projection matrix corresponding to the life cycle graph. **Figure A2b** gives the corresponding numeric values. The model assumes female demographic dominance so that, for example, fertilities are given as female fledglings per female; thus, the fledgling number used was half the fledgling number, assuming a 1:1 sex ratio. Note also that the fertility terms (F_i) in the top row of the matrix include a term for offspring production (m_i) as well as a term for the survival of the mother (P_i) from the census (just **after** the breeding season) to the next birth pulse almost a year later, plus a term (B_i) for probability of breeding. Lambda (λ), the population growth rate, was 1.01 based on the estimated vital rates used for the matrix. Although this suggests a nearly stationary population, the value is subject to the many assumptions used to derive the transitions and should not be interpreted as an indication of the general well-being and stability of the population. Other parts of the analysis provide a better guide for assessment.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. **Sensitivity** is the effect on population growth rate (λ) of an **absolute** change in the vital rates (a_{ij}, the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, **A** [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206-225). First, sensitivities show how important a given vital rate is to population growth rate (λ), which Caswell (2001, pp. 280-298) has shown to be a useful integrative measure of overall fitness. One can use sensitivities to

assess the relative importance of the survival (P_i) and fertility (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on accurate estimation of transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth (λ) of endangered species or the "weak links" in the life cycle of a pest.

Figure A3 shows the sensitivity matrix for this analysis. In general, changes that affect one type of age class or stage will also affect all similar age classes or stages. It is, therefore, usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is that the sensitivities of λ to changes in first-year survival (0.775; 37 percent of total) and adult survival (0.622; 30 percent of total) are considerably larger than to changes in the fertility rates (33 percent for both combined). The major conclusion from the sensitivity analysis is that enhancement of early survival is the key to population viability.

Elasticity analysis

Elasticities are the sensitivities of λ to **proportional** changes in the vital rates (a_{ij}). The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity

Stage	1	2
1	$P_1*m_1*B_1$	P_a*m_a
2	P_1	P_a

Figure A2a. Symbolic values for the matrix cells. The top row is fertility with compound terms describing probability of breeding (B_i), survival of the mother (P_i) and offspring production (m_i). Note that the matrix is not purely age-classified because of the multi-age stage (No. 2) denoted by the self-loop term in the bottom right corner.

Stage	1	2
1	0.351	0.822
2	0.322	0.609

Figure A2b. Numeric values for the matrix cells.

Figure A2. The input matrix of vital rates, **A** (with cells a_{ij}) corresponding to the purple martin life cycle graph (**Figure A1**). a) Symbolic values. b) Numeric values.

40

Stage	1	2
1	0.378	0.304
2	0.775	0.622

Figure A3. Sensitivity matrix, **S**. The two transitions to which λ of purple martin is most sensitive are highlighted: first-year survival and adult survival (Cells s_{21} and s_{22}). Unlike the elasticities (**Figure A4**) the sensitivities do not sum to one.

conclusions results from the weighting of the elasticities by the value of the original vital rates (the a_{ij} arc coefficients on the graph or cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species. It is important to note that elasticity as well as sensitivity analysis assumes that the magnitude of changes (perturbations) to the vital rates is small (i.e., that changes occur near to equilibrium). Large changes require a reformulated matrix and reanalysis.

Elasticities for purple martin are shown in **Figure A4**. The λ of purple martin was most elastic to changes in adult survival (37 percent), followed successively by first-year survival and adult fertility (both at 25 percent). Overall, survival transitions accounted for approximately 62 percent of the total elasticity of λ to changes in the vital rates. The survival rates are the key to population dynamics and are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The **stable (st)age distribution** (SSD, **Table A2**) describes the proportion of each Stage (or Age-class) in a population at demographic equilibrium.

Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SAD within 20 to 100 census intervals. For purple martin at the time of the post-breeding annual census (just after the end of the breeding season), young of the year comprise 56 percent of the population, with the adults comprising the remaining 44 percent of the population. Cochran and Ellner (1992) devised an elegant way of calculating the mean and variance of the ages of individuals in mixed-age-class stages, such as the "adult" stage in the present model. The mean age of an adult female purple martin is 2.6 (± 2.0). **Reproductive values (Table A3)** can be thought of as describing the "value" of a stage as a seed for population growth relative to that of the first (newborn) stage. The reproductive value of the first stage is always 1.0. An adult female individual is "worth" approximately two female fledglings (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams,

Stage	1	2
1	0.132	0.247
2	0.247	0.374

Figure A4. Elasticity matrix, **E** (the values sum to one). The λ of purple martin is most elastic to changes in survival of adults (Cell e_{22}) followed by first-year survival and adult fertility (both at 0.25).

Table A2. Stable stage distribution (SSD, right eigenvector). At the census, 24 percent of the population should be young of the year. Approximately 10 percent will be yearlings, and the remainder will be older females.

Stage	Description	Proportion	Mean ± sd of age of stage
1	First-year females	0.555	0 ± 0
2	Adult females	0.445	2.6 ± 2.0

Table A3. Reproductive values for females. Reproductive values can be thought of as describing the "value" of a stage as a seed for population growth, relative to that of the first (fledgling) stage, which is always defined to have the value 1.0.

Stage	Description	Reproductive values
1	First-year females	1.00
2	Adult females	2.05

1966). The cohort generation time for purple martin is 2.7 years (SD = 2.0 years).

Stochastic model

We conducted a stochastic matrix analysis for purple martin. We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the amount of stochastic fluctuation (**Table A4**).

Under Variant 1 we altered the offspring production terms (m_i) and the probability of breeding at the end of the first year (B_1). Under Variants 2 and 3 we varied survival (P_1 and P_A). Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Stage Distribution (SSD) under the deterministic model. Beginning at the SSD helps avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of running each of 100 replicate populations for 2,000 annual cycles, from a starting size of 10,000. We varied the amount of fluctuation by varying the standard deviation of the beta distribution from which the stochastic vital rates were selected. The beta distribution has the useful property of existing in

the interval zero to one, thereby avoiding problems of impossible parameter values (<0 or >1) or altered mean and variance (as when using a truncated normal distribution). For values that can range above 1.0, one can use a stretched beta distribution to provide a similar bound on the range of randomly chosen input values (Morris and Doak 2002). The default value was a standard deviation of one quarter of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Variant 3 affected the same transitions as Variant 2 (P_{21} and P_{32}) but was subjected to lower variability (SD was 1/8 rather than 1/4 of the mean). We calculated the stochastic growth rate, $log\lambda_s$, according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics. A population was considered "pseudoextinct" (Morris and Doak 2002) if it dipped below 10 individuals.

The stochastic model (**Table A4**) produced two major results. First, altering the survival rates had a much more dramatic effect on λ than did altering the fertilities. For example, under the varied fertilities of Variant 1, 43 of 100 simulated populations went pseudoextinct and 23 populations declined from their initial size. In contrast, the same degree of variation

Table A4. Summary of three variants of stochastic projections for purple martin. Each variant consisted of 100 runs, each of which ran for 2,000 annual census intervals. Stochastic vital rates were selected from a beta distribution with mean at the deterministic value and SD of 1/4 or 1/8 of the mean.

	Variant 1	Variant 2	Variant 3
Input factors:			
Affected cells	F_1	P_1	P_1 and P_a
S.D. of random normal distribution	1/4	1/4	1/8
Output values:			
Deterministic λ	1.01	1.01	1.01
# Extinctions / 100 trials	43	100	48
Mean extinction time	1,070	186	1,275
# Declines / # surviving populations	23/57	—	19/52
Log λ_s	-0.003	-0.05	-0.003
λ_s	0.997	0.952	0.997
Percent reduction in λ	1.3	5.8	1.3

acting on survival under Variant 2 resulted in all 100 populations going pseudoextinct, with a mean time to pseudoextinction of 186 census intervals. Second, large-effect stochasticity has a negative effect on population dynamics, at least when it impacts transitions to which λ is highly sensitive and elastic. The negative effect of stochasticity occurs despite the fact that the average vital rates remain the same as under the deterministic model. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the deterministic population size expectation.

For purple martin under the survival Variant 2 with a high degree of stochasticity (SD = 1/4 of the mean), all populations went pseudoextinct. Variant 3 shows that the magnitude of fluctuation has a potentially large impact on the detrimental effects of stochasticity. Decreasing the magnitude of fluctuation decreased the severity of the negative impacts – the number of pseudoextinctions went from 100 to 48 (an additional 19 populations declined from their starting size). The reduction in detrimental effects under Variant 3 resulted in an outcome similar to that produced by high variability acting on fertility. That is, either high variability in fertility or lower variability in survival led to similar outcomes, whereas higher variability in survival led to drastic reductions in viability. These differences in the effects of stochastic variation are predictable from the sensitivities and elasticities. λ was much more elastic to changes in first-year and adult survival, P_1 and P_A, than it was to changes in the entire set of fertilities, F_i.

These results suggest that populations of purple martin are relatively tolerant to stochastic fluctuations in offspring production (due, for example, to annual climatic change or to human disturbance) but extremely vulnerable to variations in survival. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may induce variation in previously invariant vital rates (such as annual survival), with consequent detrimental effects on population dynamics. Further, in the case of high sensitivity of λ to changes in first-year survival, selection may be relatively ineffective in reducing variability that surely results from a host of biotic and abiotic factors.

Potential refinements of the models

Clearly, the better the data on early survival rates, the more accurate the resulting analysis. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would incorporate forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.